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RYE RESISTANT TO LEAF RUST, STEM RUST, AND POWDERY MILDEW [1]

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INTRODUCTION

As one phase of investigations being conducted in cooperation with the Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture, the reaction of a number of varieties of rye to the leaf rust, *Puccinia dispersa* Erikss. and Henn., is being studied. Some of the results of this study have been reported in a paper by Mains and Leighty (*5*). [3]

In connection with these studies, a number of plants selected for resistance to leaf rust were grown in the greenhouses of the department of botany, Purdue University Agricultural Experiment Station. These became infected by powdery mildew, *Erysiphe graminis secalis* Marchal. While most of the selections were obviously quite susceptible, a few were not infected appreciably by this pathogen. It therefore seemed important that these few selections be more thoroughly studied. In consequence, a study of the reaction of the strains of rye resulting from these selections was undertaken as part of the investigations being conducted on disease resistance by the department of botany of the Purdue University Agricultural Experiment Station. This paper gives the results of three years' investigation of the reaction to leaf rust (*Puccinia dispersa*), stem rust (*Puccinia graminis secalis* Erikss. and Henn.), and mildew (*Erysiphe graminis secalis*) of the lines of rye originating from two leaf-rust and mildew resistant plants.

METHODS

The culture of the leaf rust of rye employed in these studies was obtained from a single urediniospore obtained from rusted rye at La Fayette, Ind. Although there is at present no evidence of the existence of strains of the leaf rust of rye, the presence of a number of forms in such rusts as *Puccinia graminis* (*3, 9, 10*) and in *Puccinia triticina* (*4*) suggests the likelihood of their occurrence in the leaf rust of rye. To avoid confusion which might arise if the culture used were a mixture of forms, it seemed advisable to make certain that only one strain of the rust was being employed by starting from a single urediniospore.

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[2] The writer wishes to acknowledge the advice and criticism of C. E. Leighty, H. S. Jackson, and H. B. Humphrey, and the help of Leroy Compton in the inoculation of the large number of plants studied.

[3] Reference is made by number (italic) to "Literature cited," p. 221.

The method employed in making single-spore cultures of leaf rusts has already been described (*6*), but will be reviewed here. Urediniospores of a collection of the rust were gently dusted into a Petri dish. This dish was then placed under the high power of a binocular microscope, and a single urediniospore, well separated from the others, was found. This urediniospore was picked up by means of a glass rod drawn out to a fine point, to which, when wetted, the urediniospore usually adheres. By means of this glass needle the spore was transferred to a moistened blade of a rye seedling. A number of such seedlings was inoculated in this way in order to make sure of obtaining infection. These were placed in moist chambers for 48 hours. After being removed, they were observed daily. On the appearance of the first sign of a uredinium all the other inoculated plants were destroyed, leaving the one infected plant. From the uredinia produced on the remaining plant other rye plants were inoculated and the rust multiplied. All other leaf rust of rye was removed from the greenhouse, and only the culture from the single spore was retained.

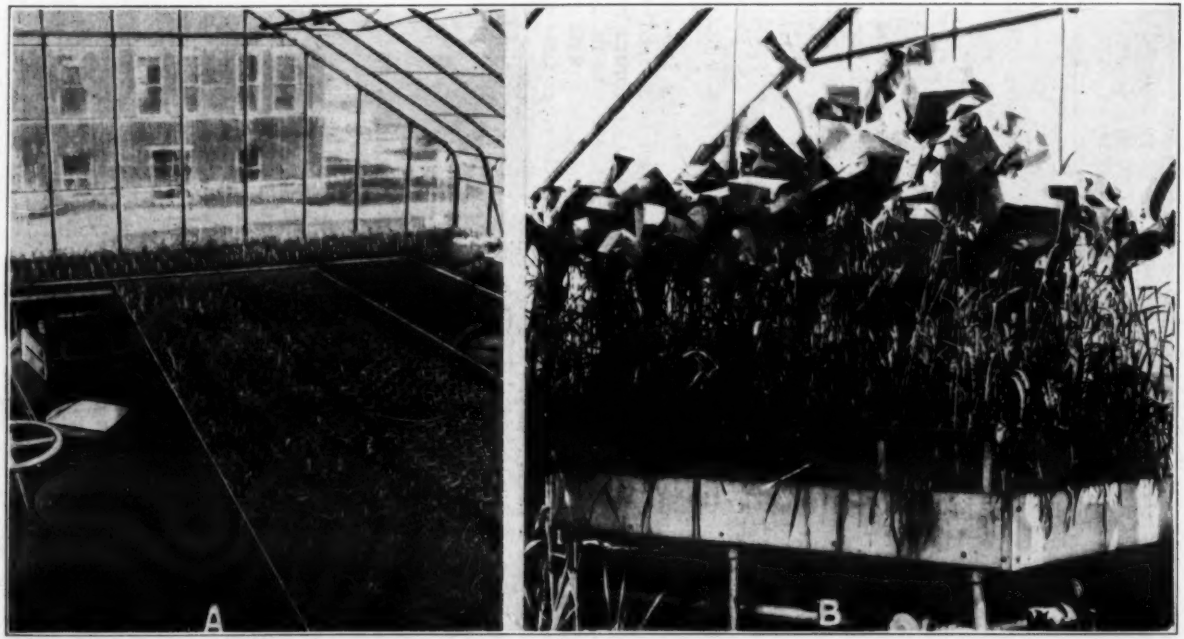
Where only a few plants were to be inoculated, the urediniospores were removed from the plants of the stock culture by means of a scalpel and placed on the moistened leaves of the plants to be tested for relative susceptibility. The inoculated plants then were placed in a chamber, the air of which could be kept practically saturated and where a temperature of approximately 20° C. was maintained. They were removed after 48 hours and placed on the greenhouse bench.

Where a large number of plants were to be inoculated (pl. 1, A), urediniospores were dusted on them. The plants were first atomized and the spores dusted on by shaking heavily rusted rye plants over them. The inoculated plants then were covered with heavy muslin, which was kept wet by occasionally spraying with water. After two days the muslin was removed. In this way it was possible to inoculate a large number of plants without removing them from the greenhouse bench.

In like manner a single-spore culture of stem rust of rye, *Puccinia graminis secalis*, of the rust collected at LaFayette, Ind., was obtained, and similar methods were used in inoculating with it.

No attempt was made to obtain a single-spore culture of powdery mildew of rye, for it was so prevalent in the greenhouse that it would have been very difficult to maintain a culture pure. The mildew spread and developed vigorously without any special methods of inoculation, susceptible plants becoming heavily mildewed in a short time. However, in order to be sure that freedom from mildew really was due to resistance, all plants were inoculated by shaking heavily mildewed plants over the series and then covering with wet mulsin for 48 hours.

Seed of the rye to be studied for relative susceptibility to rust was sown in the early fall in 3 or 4 inch pots, (pl. 1, A). The plants usually were first inoculated with leaf rust when the third or fourth leaf had developed. Sometimes this was followed by a second inoculation. After taking notes on their reaction to leaf rust, the plants were inoculated with mildew and notes were taken on their relative susceptibility to this disease. Then, in general, only those plants



A. Seedlings of rye ready for inoculation. The spores of leaf rust, mildew, or stem rust were dusted on and the plants then covered with wet muslin for 48 hours
B. Selections made for disease resistance, transplanted to greenhouse bed. To insure selfing, the heads were bagged just before blossoming

showing resistance to leaf rust and mildew, were inoculated with stem rust, and notes were taken concerning their susceptibility to this rust.

Those plants showing the most promise in resistance were then transplanted to the greenhouse bed and grown to maturity. When the plants were about to blossom, the heads of each plant were enclosed together in a heavy Manila paper bag (pl. 1, B) so as to protect them from foreign pollen and to bring about self fertilization. When crosses were desired, one or more heads from two adjacent plants were bagged together.

RESULTS FROM SELECTIONS OF NORTH CAROLINA ABRUZZES

As has been previously reported (*5*), plants resistant to the leaf rust of rye were found in each of the 68 selections and varieties studied in the autumn of 1921. From those showing resistance, 69 selections were made and were grown to maturity in the greenhouse. These included 41 plants of Abruzzes, 2 of Giant Winter, 1 of Henry, 1 of Invincible, 3 of Ivanov, 2 of Mammoth Winter, 1 of Mexican, 4 of Petkus, 3 of Rosen, 4 of St. John, 4 of Star, and 1 of Von Ruemker. During the winter all but two of these plants became heavily mildewed with *Erysiphe graminis secalis*.

The two plants showing no mildew were two of the leaf-rust-resistant selections made from Abruzzes rye grown from seed obtained from G. M. Garren, of the North Carolina Experiment Station. That these plants were in reality highly resistant to mildew and had not escaped infection was shown by inoculating with the mildew. Other plants of Abruzzes inoculated at the same time and in the same way became heavily mildewed.

On account of the high resistance shown by these two plants to both leaf rust and mildew, they were isolated from the rest in another greenhouse. Several of the heads of each plant were bagged to prevent cross pollination. The remaining heads of the two plants were bagged together and allowed to cross-pollinate. Only seven seeds were produced from the selfed heads of one plant, and none from the selfed heads of the other. From the cross-pollinated heads 286 seeds were obtained.

In the autumn of 1922, the 293 seeds obtained from the two leaf-rust and mildew resistant plants were sown in the greenhouse. Of these 284 grew and were inoculated with leaf rust of rye. After obtaining notes on the reaction of these plants to leaf rust they were reinoculated with the rust and the notes on relative susceptibility checked. Following this the whole series was twice inoculated with mildew and notes obtained on the susceptibility of each plant.

As a number of the plants were resistant to both leaf rust and mildew, it seemed advisable to study their reaction to other diseases. A culture of stem rust from a single urediniospore was developed and was sown on a part of the plants, especially those showing resistance to both leaf rust and mildew. This also was followed by a reinoculation to check results.

Among the plants inoculated, several degrees of susceptibility to all three diseases were noted. For each disease, the host reaction ranged from high susceptibility to very high resistance. In order to give the results obtained, it is necessary to classify here the degrees

of host reaction to leaf rust. In a previous paper (*5*) the reaction of rye to leaf rust was classified and illustrated. Susceptibility was there divided into five different groups denoted by the symbols 0 to 4. A similar classification is used here, and it may be described as follows:

Symbol	Classes of host reaction	Types of infection
0	Immune or highly resistant	No uredinia formed; small flecks, chlorotic and necrotic areas more or less prevalent. (Plate 2, *a*.)
1	Very resistant	Uredinia few, small, accompanied by necrosis immediately surrounding uredinia. Necrotic areas often produced without uredinia. (Plate 2, *b* and *c*.)
2	Moderately resistant	Uredinia fairly abundant, moderate to large in size, but always in necrotic areas. Infected areas generally producing uredinia. (Plate 2, *d*.)
3	Moderately susceptible	Uredinia abundant, moderate in size, producing no necrosis, but sometimes causes slight chlorosis. (Plate 2, *e*.)
4	Very susceptible	Uredinia abundant, large, no necrosis or chlorosis immediately surrounding uredinia. Infected areas sometimes occurring as green islands surrounded by some chlorosis. (Plate 2, *f*.)

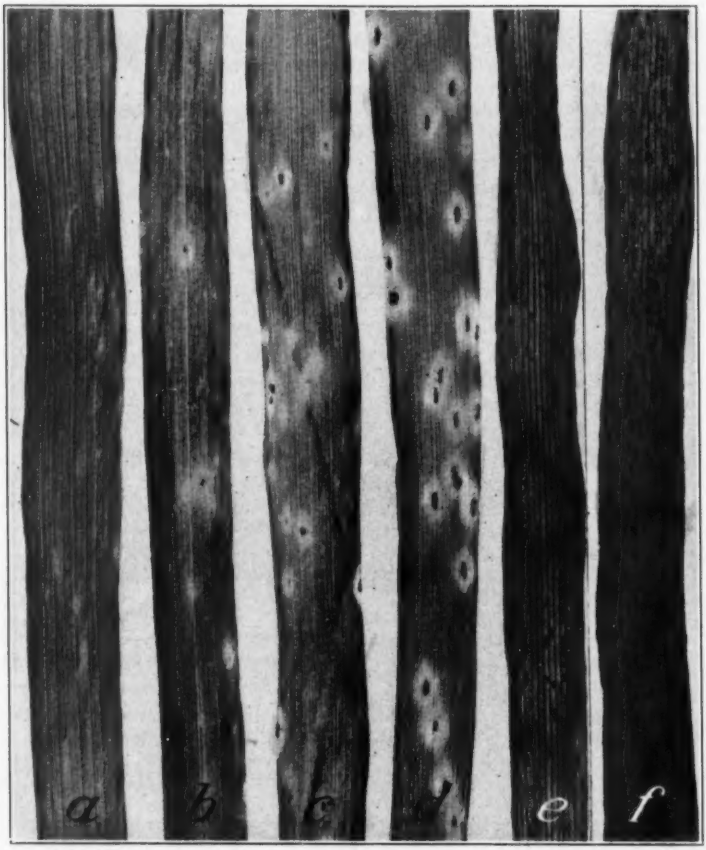
For the classes of reaction of rye to stem rust similar types are recognized, agreeing with the classification used by Stakman and Levine (*9*) and others for reaction of wheat and other cereals to stem rust. The types of infection for the five classes of host reaction may be described as follows:

Symbol	Classes of host reaction	Types of infection
0	Highly resistant	No uredinia developed; small flecks, chlorotic and necrotic areas more or less present. (Plate 3, A, *a*.)
1	Very resistant	Uredinia few, minute, in necrotic areas; necrotic areas sometimes without uredinia. (Plate 3, A, *b* and *c*.)
2	Moderately resistant	Uredinia fairly abundant, small to mid-size, usually accompanied by necrosis or chlorosis. (Plate 3, A, *d*.)
3	Moderately susceptible	Uredinia abundant, medium to large in size; coalescence infrequent; occasionally accompanied by slight chlorosis. (Plate 3, A, *e*.)
4	Very susceptible	Uredinia very abundant, large, confluent; no necrosis, but occasionally with some chlorosis and uredinia sometimes in green islands. (Plate 3, A, *f*.)

In like manner the reaction of rye to mildew may be classified into five classes as follows:

Symbol	Classes of host reaction	Types of infection
0	Highly resistant	No apparent development of mildew. Occasional development of very slight amount of mycelium and haustoria, usually to be noted microscopically only by small chlorotic flecks. (Plate 3, B, *a*.)
1	Very resistant	Slight development of mycelium, with little or no sporulation. (Plate 3, B, *b*, and Plate 4, *a*.)
2	Moderately resistant	Moderate development of mycelium, with light sporulation. (Plate 3, B, *c*, and Plate 4, *b*.)
3	Moderately susceptible	Moderate to heavy development of mycelium, and moderate sporulation. (Plate 3, B, *d* and plate 5, A.)
4	Very susceptible	Heavy development of mycelium, and abundant sporulation. (Plate 3, B, *e*, and plate 5, B.)

Table I gives the results obtained by inoculating with leaf rust and mildew the 7 plants obtained from the 2 selfed leaf-rust and mildew resistant selections and the 277 plants obtained by cross pollination between them. Of these, 166, for the most part resistant to leaf rust and mildew, were tested for their reaction to stem rust, and the results are recorded in Table I.

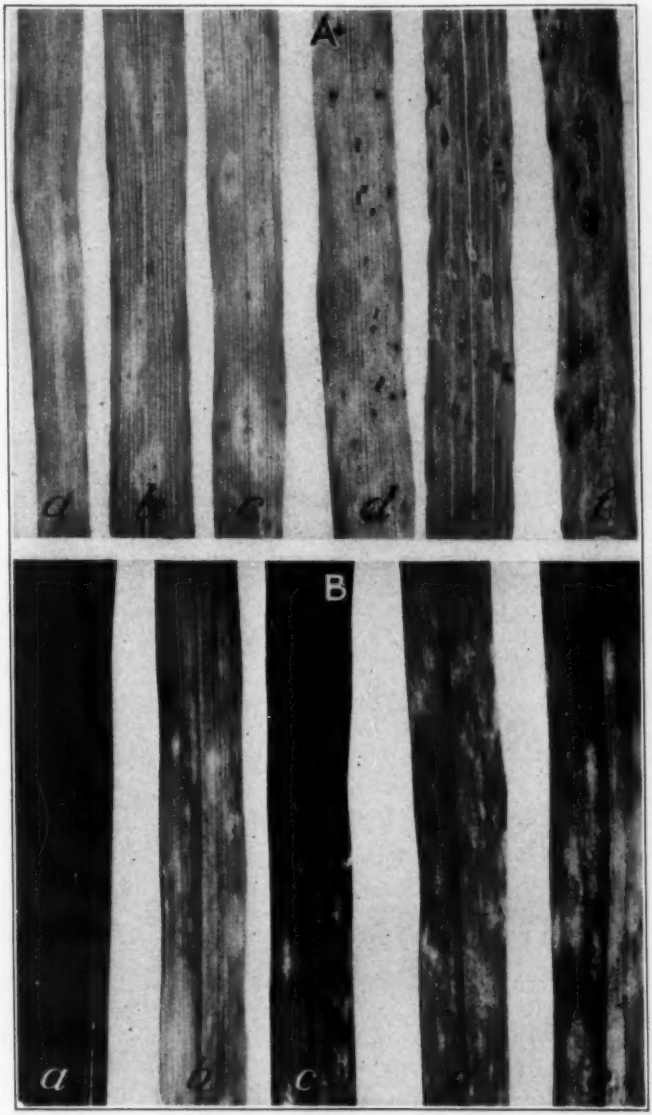


Types of infection of rye by leaf rust, *Puccinia dispersa:*

a. Highly resistant, 0. Infection indicated only by flecks or small necrotic areas
b. Very resistant, 1. Few small uredinia in necrotic areas
c. Same as *b*.
d. Moderately resistant, 2. Uredinia fairly abundant in necrotic areas
e. Moderately susceptible, 3. Abundant uredinia of moderate size. Sometimes accompanied by slight chlorosis, which is not shown here
f. Very susceptible, 4. Uredinia very abundant, and of large size. Little or no chlorosis

EXPLANATORY LEGEND FOR PLATE 3

A. Types of infection of rye by stem rust, *Puccinia graminis secalis:*
   a. Highly resistant, 0. No uredinia developed. Infection indicated by only necrotic or chlorotic areas
   b. Very resistant, 1. Few small uredinia in necrotic or chlorotic areas
   c. Same as *b*
   d. Moderately resistant, 2. Uredinia fairly abundant, medium in size and accompanied by necrosis or chlorosis
   e. Moderately susceptible, 3. Uredinia abundant, and medium to large in size, accompanied occasionally by slight chlorosis
   f. Very susceptible, 4. Uredinia very abundant, confluent
B. Types of infection of rye by powdery mildew, *Erysiphe graminis secalis* (slightly enlarged):
   a. Highly resistant, 0. No apparent development, except by occasional slight chlorosis
   b. Very resistant, 1. Slight development
   c. Moderately resistant, 2. Moderate development
   d. Moderately susceptible, 3. Development fairly heavy
   e. Very susceptible, 4. Very heavy development



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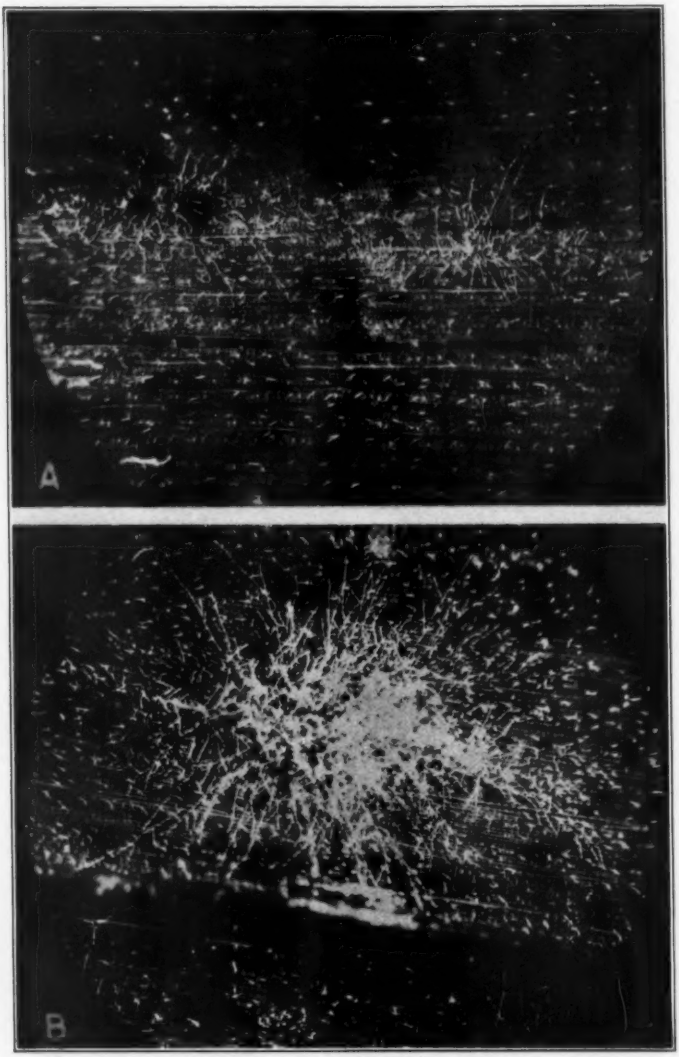
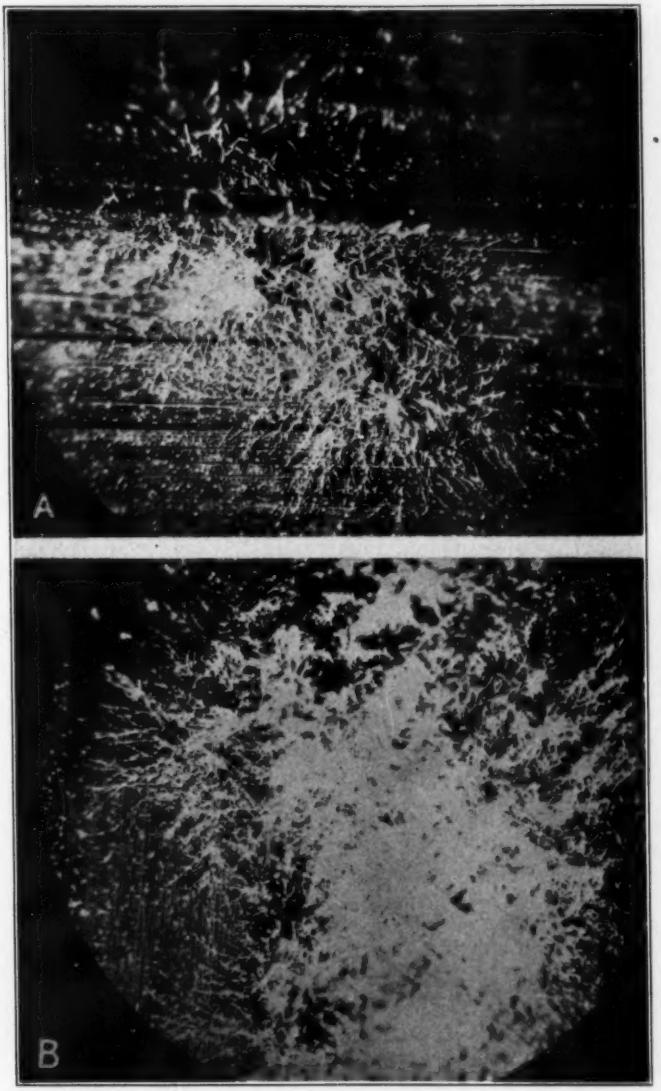


Types of infection of rye by powdery mildew, *Erysiphe graminis secalis* (× 25):
A.—Very resistant, 1. Development of mycelium slight. Little or no sporulation
B.—Moderately resistant, 2. Moderate development of mycelium. Slight sporulation



Types of infection of rye by powdery mildew, *Erysiphe graminis secalis* (× 25)

A.—Moderately susceptible, 3. Moderate development of mycelium, and moderate sporulation

B.—Very susceptible, 4. Heavy development of mycelium, and very heavy sporulation

TABLE I.—*Reaction to leaf rust (Puccinia dispersa), stem rust (Puccinia graminis secalis), and mildew (Erysiphe graminis secalis) of the first generation of progeny of a selfed plant and a number of crossed plants of rye selected for resistance*

Pathogen and source	Number of plants in each reaction class					Total number of plants
	0	1	2	3	4	
Puccinia dispersa:						
Plant A, selfed[a]	1	2	----	1	3	7
Plant A×B	34	38	7	20	18	117
Plant B×A	40	57	7	34	22	160
Erysiphe graminis secalis:						
Plant A, selfed	4	1	2	----	----	7
Plant A×B	82	10	14	8	3	117
Plant B×A	108	13	26	11	2	160
Puccinia graminis secalis:[b]						
Plant A, selfed	1	----	----	1	----	2
Plant A×B	16	23	12	13	10	74
Plant B×A	20	37	18	9	8	92

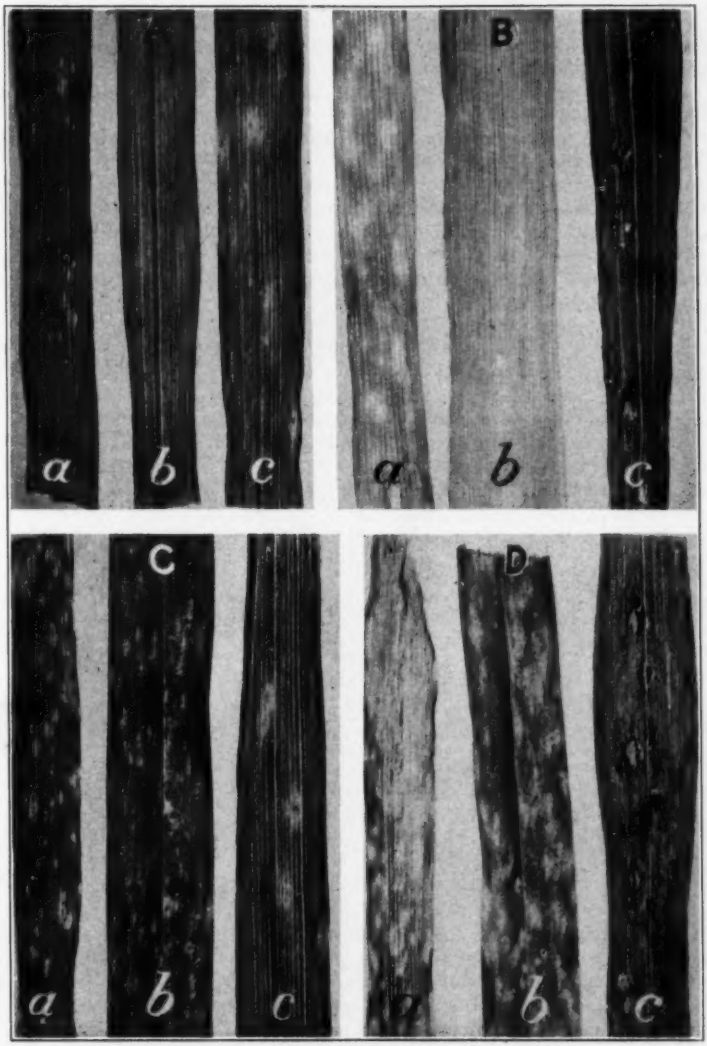
[a] Plant B, selfed, was sterile.
[b] Only plants resistant to both *Puccinia dispersa* and *Erysiphe graminis secalis* were studied for susceptibility to *Puccinia graminis secalis*.

As parent plant A, when selfed, produced some offspring susceptible and some resistant to leaf rust, it evidently was heterozygous for susceptibility to this rust. Unfortunately, no seed was produced by plant B when selfed. If types 0, 1, and 2 are considered as resistant, and types 3 and 4 as susceptible, plant A when crossed with B produced 79 resistant individuals and 38 susceptible. Plant B, when crossed with A, gave a very similar proportion, i. e., 104 resistant and 56 susceptible.

All seven plants resulting from selfing plant A were resistant to mildew. However, the crosses between resistant plants A and B resulted in the production of susceptible individuals. Plant A crossed with B gave 106 resistant and 11 susceptible hybrids. Plant B, crossed with A, gave a similar proportion, i. e., 147 resistant and 13 susceptible. While the proportion of resistant to susceptible plants is much higher in this case than with leaf rust, it is evident that here also resistance must be dominant.

Of the two individuals from selfed plant A which were tested with stem rust, one was resistant and the other susceptible. Of the 117 plants from the cross between A and B, 74 were tested for reaction to stem rust; 51 were resistant and 23 susceptible. Of the 160 individuals from the cross between plants B and A, 92 were tested for relative susceptibility to stem rust; 75 were resistant and 17 susceptible. These figures clearly show a difference in the ratio of resistant to susceptible individuals from the A×B cross when compared with those from the B×A cross. Possibly this may be due to the smaller number of plants used, as, for the most part, only those resistant to both leaf rust and mildew were studied. It is apparent, however, that resistance to stem rust also is dominant in this material.

From Table I it is obvious that some of the plants must have shown different types of reaction to the different diseases, as the number of resistant and susceptible individuals were not the same for each. Such was the case. Some were highly resistant to all three (pl. 6, A). Some showed themselves highly resistant to one or two and moderately resistant to the others. Some were highly resistant to



Some of the combinations of reaction to leaf rust, mildew, and stem rust, noted in plants of rye

A.—Plant resistant to leaf rust (*a*), resistant to mildew (*b*), and resistant to stem rust (*c*)
B.—Plant resistant to leaf rust (*a*), resistant to mildew (*b*), and susceptible to stem rust (*c*)
C.—Plant resistant to leaf rust (*a*), susceptible to mildew (*b*), and resistant to stem rust (*c*)
D.—Plant resistant to leaf rust (*a*), susceptible to mildew (*b*), and susceptible to stem rust (*c*)

one or two and susceptible to the others (pl. 6, B, C, D). A few proved to be susceptible to both leaf rust and mildew. Table II gives the different combinations of susceptibilities to leaf rust, mildew, and stem rust shown by the plants studied, and the number of plants found having each combination.

As resistance to all three diseases apparently is dominant, and the majority of plants were resistant to each, the number combining resistance to two or three of these diseases is naturally rather large. Thus out of 284, 145 showed either type 0 or 1 to leaf rust and mildew, and of this group 73 were also highly resistant (0 or 1) to stem rust and therefore also highly resistant to all three diseases. Only 6 were susceptible (type 3 or 4) both to leaf rust and mildew, their reaction to stem rust not being studied. The remainder of the plants showed various combinations of resistance and susceptibility to the three diseases.

TABLE II.—*Combinations of classes of reaction to leaf rust (Puccinia dispersa), mildew (Erysiphe graminis secalis), and stem rust (Puccinia graminis secalis), shown by plants of rye, in 1922*

Combination of classes of reaction			Number of plants showing combination	Combination of classes of reaction			Number of plants showing combination
Leaf rust	Mildew	Stem rust		Leaf rust	Mildew	Stem rust	
0	0	0	12	1	1	3	1
0	0	1	13	1	2	0	2
0	0	2	14	1	2	1	7
0	0	3	11	1	2	2	3
0	0	4	8	1	2	3	2
0	0	(*)	3	1	3	0	3
0	1	0	1	1	3	1	4
0	1	1	1	1	3	4	1
0	2	1	4	1	3	(*)	3
0	2	3	2	1	4	0	1
0	2	4	1	2	0	(*)	9
0	3	0	1	2	1	(*)	2
0	3	4	1	2	2	(*)	2
0	4	2	2	2	3	(*)	1
0	4	4	1	3	0	(*)	32
1	0	0	13	3	1	(*)	8
1	0	1	29	3	2	(*)	12
1	0	2	10	3	3	(*)	2
1	0	3	7	3	4	(*)	1
1	0	4	4	4	0	(*)	28
1	0	(*)	1	4	1	(*)	5
1	1	0	3	4	2	(*)	7
1	1	1	1	4	3	(*)	3
1	1	(*)	2	4	4	(*)	0

*Not studied.

Of the plants studied for disease reaction in 1922, 102 were transplanted to the greenhouse bench and grown to maturity. All of these were allowed to self in the spring of 1923, part of the heads of each plant being bagged to prevent cross-pollination. From these plants 174 seeds were obtained as follows: Seventy-one plants produced no seed; nine produced 1 each; eight, 2; two, 3; two, 4; two, 6; two, 9; one, 15; one, 16; one, 17; two, 18; and one, 21.

Besides selfing the plants, crosses between some of the most resistant were attempted. This was done by bagging together the heads of two plants and allowing them to cross-pollinate. This method, of course, does not prevent some selfing, but on account of the low self-fertility it seemed desirable to use this method in an attempt to obtain an abundance of seed from resistant plants.

In the autumn of 1923, the seed obtained was sown in the greenhouse, and each plant obtained was first inoculated and studied for susceptibility to leaf rust. Following this, most were inoculated and studied for susceptibility to stem rust. Unfortunately, during the summer of 1923, the culture of mildew of rye was lost and none was obtained for use that fall. Consequently, data on the relative susceptibility to this disease is therefore lacking for this year.

Table III gives the data obtained for the reaction of the selfed plants. The progeny of the 29 selfs were studied for relative susceptibility to leaf rust. The progeny of nine selfs included both susceptible and resistant individuals, indicating that the parents were heterozygous for susceptibility. Two others consisted of a single susceptible individual, while 18 of the parents gave resistant progeny only.

Reaction to stem rust was studied in the progenies of 28 selfed plants. The progenies of 13 of these showed both susceptible and resistant plants. Two, S9–2 and 125A–19, showed only susceptible plants, consisting of two and eight plants, respectively. Since the parent plants were resistant this would indicate that they were also heterozygous. The remaining 13 produced only resistant plants.

Comparing the results obtained for the two rusts, eight of the selfed parents are plainly heterozygous for susceptibility to both rusts. Eleven had progeny which were entirely resistant to one rust, while some or all were susceptible to the other. It is true that nine had progeny entirely resistant to both rusts, but so few plants were produced that no conclusions can be safely drawn concerning homozygosity.

TABLE III.—*Reaction to leaf rust (Puccinia dispersa) and stem rust (Puccinia graminis secalis), in 1923, of progeny obtained by selfing rye plants which were resistant in 1922.*

Pedigree No. of parent	Class of reaction of parent plants 1922		Number of plants from selfs under each class of reaction									
			Leaf rust					Stem rust				
	Leaf rust	Stem rust	0	1	2	3	4	0	1	2	3	4
S9–2 [a]	1	0	----	2	----	----	----	----	----	----	----	2
125A–6 [b]	1	0	----	4	3	1	----	----	3	3	1	1
125A–17	1	1	8	4	5	----	1	1	12	1	----	1
125A–19	1	0	1	----	----	----	----	----	1	----	----	----
125A–24	1	1	8	1	----	----	----	----	----	----	5	3
125A–27	1	1	2	1	----	----	----	3	----	----	----	----
127A–5	1	1	----	1	----	----	----	----	1	----	----	----
127A–34	1	1	----	1	----	----	----	----	----	1	----	----
127A–39	1	1	9	4	1	2	2	2	9	5	1	----
127A–43	1	1	1	----	----	----	----	1	----	----	----	----
127A–48	1	2	----	1	1	----	----	2	----	----	----	----
128B–10	1	0	1	1	----	----	----	----	1	----	1	----
128B–12	1	1	1	----	----	----	----	----	----	----	----	----
128B–14	1	1	----	3	----	----	1	----	3	----	1	----
128B–29	1	0	1	1	1	----	----	----	1	1	1	----
125B–5	1	1	3	1	----	----	----	----	1	1	1	----
125B–6	1	1	1	1	----	----	----	----	----	1	----	1
125B–10	1	1	2	9	5	2	3	5	5	6	3	----
125B–13	0	0	11	2	1	----	2	3	7	5	----	----
125B–36	0	0	1	----	----	1	----	2	----	----	----	----
125B–12	0	1	----	----	1	----	----	1	----	----	----	----
127B–20	1	0	3	1	1	----	1	1	3	1	1	----
128A–2	1	1	----	----	----	----	1	----	1	----	----	----
128A–3	1	1	6	----	----	----	----	1	1	3	1	----
128A–5	1	1	8	6	----	----	1	2	7	2	3	----
128A–9	1	0	1	1	----	----	----	----	----	1	1	----
128A–13	0	2	1	----	----	----	----	1	----	----	----	----
128A–34	1	1	----	----	----	1	----	----	1	----	----	----
128A–35	1	0	6	7	4	----	----	2	8	2	2	2

[a] Selfed two years. [b] The following selfed one year: F_2 from crosses of original selections.

In all cases where only resistant individuals were produced, the number was so small that it is rather doubtful whether any conclusions can be drawn concerning the genetic constitution of the parents. This, with the fact that such a large proportion of the selfs produced no seed, makes it seem extremely probable that part or all of those producing only a few resistant individuals also were heterozygous for susceptibility. It is even possible that homozygous plants may have been completely sterile in almost all cases.

From the selfed resistant plants, 159 were grown and tested for susceptibility to both leaf rust and stem rust. Of these 111 were resistant (classes 0, 1, 2) to both rusts. One plant was susceptible (classes 3, 4) to both disease. Thirty-one plants were resistant to leaf rust and susceptible to stem rust, and 16 plants were resistant to stem rust and susceptible to leaf rust. Here again is shown independent inheritance of resistance to the two diseases.

As shown by Table IV, of the 28 crosses between resistant individuals, 17 produced progenies consisting of plants both susceptible and resistant to leaf rust. The remaining 11 crosses in which all individuals were resistant, however, produced only a few plants each.

TABLE IV.—*Reaction to leaf rust (Puccinia dispersa) and stem rust (Puccinia graminis secalis), in 1923, of the first-generation progeny of crosses[a] between rye plants resistant in 1922*

Pedigree number cross	Classes of reaction of parent plants 1922				Number of F_1 plants under each class of reaction									
	Leaf rust		Stem rust		Leaf rust					Stem rust				
	A[a]	B[a]	A[a]	B[a]	0	1	2	3	4	0	1	2	3	4
2344[b]	1	1	1	0	6	9	3	----	2	2	15	1	----	----
2345[b]	1	1	0	1	13	5	----	1	6	5	13	6	----	----
2346	1	1	1	1	6	2	----	----	----	2	3	1	1	1
2347[b]	1	1	1	0	4	----	1	----	----	----	2	----	2	----
2348[b]	1	1	0	1	2	----	----	----	----	1	1	----	----	----
2349	1	0	1	0	2	----	----	----	----	----	1	----	----	----
2350[b]	1	0	1	0	8	10	3	----	3	5	10	2	3	2
2351[b]	0	1	0	1	9	9	3	----	4	4	17	----	1	1
2352	1	1	1	1	6	7	3	7	5	3	16	1	----	----
2353[b]	1	1	1	1	2	1	----	----	----	----	----	----	----	----
2354[b]	1	1	1	1	9	----	----	----	----	----	8	----	----	1
2355	0	1	0	1	15	3	4	2	1	2	20	2	----	----
2356[b]	1	1	1	0	4	1	----	1	----	----	----	----	----	----
2357[b]	1	1	0	1	2	1	----	----	----	----	----	----	----	----
2358[b]	1	1	0	0	8	3	3	2	3	2	13	1	----	----
2359[b]	1	1	0	0	----	----	----	----	2	----	----	----	----	----
2360	1	1	4	1	20	6	1	4	1	2	38	1	----	----
2361[b]	1	1	0	1	1	----	1	----	1	----	----	----	----	----
2362[b]	1	1	1	0	1	----	----	----	1	----	----	----	----	----
2363	1	1	1	2	19	6	3	3	3	2	28	3	----	----
2364	1	1	1	0	9	5	3	2	1	----	----	----	----	----
2365	1	1	0	0	1	1	----	2	----	----	----	----	----	----
2366	1	1	0	0	30	5	6	11	17	----	----	----	----	----
2367	1	1	0	0	----	1	1	----	----	----	----	----	----	----
2368[b]	1	1	1	1	13	4	----	1	1	----	----	----	----	----
2369[b]	1	1	1	1	18	6	1	1	4	----	19	2	----	----
2370[b]	1	1	1	1	18	6	1	1	4	----	----	----	----	----
2371[b]	1	1	1	1	1	4	2	1	----	----	----	----	----	----

[a] Crosses were made by bagging together heads of two rye plants. Column A gives the class of reaction of the female parent and B that of the male parent.

[b] Bracketed numbers are reciprocal crosses; that is, heads bagged together reciprocally behaving as female and male parents in the cross. In those not bracketed the head of only one plant formed seed.

Of the 15 crosses studied for reaction to stem rust, 4 produced progeny consisting of both susceptible and resistant plants, while 11 produced only resistant plants. In this connection, it is interesting to note that cross 2360, made by bagging heads of a plant highly susceptible (class 4) to stem rust with heads of a very resistant plant (class 1), produced 41 plants, all resistant. This, therefore, is further evidence of the dominance of resistance. This again illustrates the difficulty of drawing conclusions concerning the zygotic constitution of resistant plants. The resistant parent of the cross might have been homozygous for resistance. However, the selfs of both parents were sterile, so no definite conclusions can be drawn.

Of the plants obtained from the crosses, 265 were studied for relative susceptibility to both leaf rust and stem rust. Of these, 213 were resistant (classes 0, 1, 2) to both rusts; 10 were resistant to leaf rust and susceptible to stem rust, 41 proved susceptible to leaf rust and resistant to stem rust; only 1 was susceptible to both rusts.

Of the parents used in the crosses, only a few produced seed when selfed. Of the crosses, there were only 10 in which both parents produced selfed seed. In only one of these were all of the progeny from both parents resistant (nine plants from one parent and one from the other), and in this case the cross gave both resistant and susceptible plants, indicating that one or both parents were in reality heterozygous, a fact not shown in the selfs because of the small number of seed produced.

Of the plants studied for relative susceptibility to leaf rust and stem rust in 1923, the most promising were transplanted to the greenhouse bed and grown to maturity. Of these, 165 were bagged separately to prevent cross pollination. It was hoped that of this number a few at least might prove more self-fertile than hitherto. The results obtained, however, were very disappointing. Of the 165 selfed plants, only 9 produced seed, the most produced by any one plant being 11 and the total number for all 9 plants being 34.

From the 34 seeds obtained by selfing 172 plants in the spring of 1924, 26 plants were obtained in the autumn of the same year and studied for susceptibility to leaf rust, stem rust, and mildew. Fifteen of these were from five selfs of resistant plants from the previous year's crosses (2345, 2351, 2352, 2354). All showed more or less resistance to the three diseases. The remaining 11 plants were from one selfed plant (128A–35–5) of a line which had been selfed twice following the original cross between the resistant plants in 1922. All 11 plants were resistant to both leaf rust and stem rust. To mildew, on the other hand, they were all more or less susceptible (classes 3 or 4). An examination of the records of this selfed line shows that the original plant was susceptible to mildew. Susceptibility to this disease being apparently recessive, all the plants should be susceptible. Whether this line also is homozygous for resistance to both rusts is a question which can not be settled with certainty because of the small number of plants.

It seems probable, however, that the line is now homozygous for resistance to leaf rust, for the 17 plants of the previous generation were all resistant to leaf rust (Table III, 128A–35). Table III, however, shows that this line was segregating for susceptibility to stem rust in 1923. While the 1924 results indicate that plant

128A–35–5 also may have been homozygous for resistance to stem rust, the small number of individuals in the 1924 progeny leaves some doubt.

It is evident in this study of the progeny derived from the two original resistant selections from the North Carolina strain of Abruzzes, that the attempt to purify for resistance to these diseases has been frustrated repeatedly by the lack of self-fertility coupled with the dominance of resistance to each disease. Continued selfing has resulted in a reduction to 26 plants from a population of 284 in 1922. Further selfing among these is likely to result in the complete loss of the pedigreed lines, unless the 11 plants from 128A–35 may indicate a line of a fair self-fertility, but this line has the defect of being susceptible to mildew. Crosses between the resistant selections of 1924, however, very probably will multiply the number of individuals and with a much greater probability of the combinations being made between homozygous resistant individuals.

SELECTIONS FROM ABRUZZES C. I. 40–59 [4]

In the spring of 1922, one of the selections of rye for leaf rust resistance, when selfed in the greenhouse of the Purdue University Agricultural Experiment Station at La Fayette, Ind., produced 49 seeds. This selection (S2229) was made from a strain of Abruzzes, C. I. 40–59, received from C. E. Leighty (*5*), which had been selected and grown at the Arlington Experiment Farm, near Washington, D. C. Selection S2229 was outstanding in the number of seeds formed. The largest number formed by any other selfed plant of the selections for resistance in the rye varieties was 7, and the total number of seeds produced by the 22 selfed selections which formed seed was 50, many of the selections producing no seed.

In the autumn of 1922, the 49 seeds from selection S2229 were sown in the greenhouse and 41 plants were obtained. These were inoculated with the leaf rust of rye. Of these, 26 proved to be resistant and 15 susceptible. Sixteen of the most resistant were transplanted to the greenhouse bed. Five plants died, killed by anthracnose. Of the remainder, five developed very poorly. The remaining six were all selfed in the spring of 1923, and a total of 292 seeds were obtained.

In the autumn of 1923, part of this seed was sown in the greenhouse and it produced 98 plants, representing 5 resistant plants of the previous generation. These were all inoculated with the leaf rust of rye, and the results are given in Table V. Of the 98 individuals, only one was susceptible and families from S2229–11, 23, and 34 were especially outstanding for the high resistance shown by all the individuals comprising them. The plants of these three families were all transplanted to the greenhouse bed and grown to maturity. Of these, 19 of the most vigorous and promising were bagged for selfing. From these 591 seeds were obtained.

In the autumn of 1924, part of this seed was sown in the greenhouse and 204 plants were obtained. These were inoculated with leaf rust with the results shown in Table VI. According to this, all 204 of the plants were highly resistant to leaf rust. These results,

[4] The first number is the accession number, Office of Cereal Investigations. The second number represents a selection made in 1918.

taken with the high resistance of most of the families of the previous generation, would indicate that a line of rye has been isolated homozygous for resistance to leaf rust.

TABLE V.—*Reaction of the progeny of two-year selfs of rye, Abruzzes C. I. 40–59, to leaf rust, Puccinia dispersa*

Parent No.	Number of individuals in each reaction class					Total
	0	1	2	3	4	
S2229–1	10	2	2	0	0	14
S2229–11	16	6	0	0	0	22
S2229–23	24	5	0	0	0	29
S2229–34	10	3	0	0	0	13
S2229–35	6	13	0	0	1	20

TABLE VI.—*Reaction of the progeny of third-year selfs of rye, Abruzzes C. I. 40–59, to leaf rust (Puccinia dispersa), stem rust (Puccinia graminis secalis), and mildew (Erysiphe graminis secalis)*

Parent No.	Number of individuals in each class of reaction								Total
	Leaf rust		Stem rust		Mildew				
	0	1	0	1	0	1	2	3	
S2229–11–1	4	.....	4	.....	.....	3	1	.....	4
S2229–11–3	30	.....	16	14	.....	7	19	4	30
S2229–11–7	23	.....	19	4	3	19	1	.....	23
S2229–11–9	40	.....	10	8	.....	13	9	.....	[a] 40
S2229–11–16	14	.....	10	.....	.....	12	2	.....	[a] 14
S2229–23–29	34	.....	31	.....	.....	25	9	.....	[a] 34
S2229–34–3	41	3	44	.....	1	32	11	.....	44
S2229–34–5	6	.....	6	.....	.....	6	.....	.....	6
S2229–34–7	9	.....	9	.....	.....	4	5	.....	9

[a] Plants of each of these families died before inoculation with stem rust. Only a part of family S2229–11–9 inoculated with stem rust and mildew.

It is to be noted that this line of rye has possessed from the start a remarkably high self-fertility. Since the resistant strain from North Carolina Abruzzes lacked this character, it was decided to study this material for susceptibility to stem rust and mildew, with the idea of using it in hybrids with the North Carolina strain. Inoculation with stem rust and mildew, however, resulted in discovering (Table VI) that all of the plants were hightly resistant to stem rust and were moderately or highly resistant to mildew. As this is the first thorough study of this material for susceptibility to stem rust and mildew, one can not be sure whether this line is also homozygous for resistance to these diseases or of the manner of inheritance of the resistance. However, the general uniformity of resistance in this material strongly suggests that the families listed in Table VI are homozygous for stem rust and mildew resistance as well as for leaf-rust resistance.

Selection S2229 and the lines originating from it have been remarkable for the pronounced self-fertility which they have shown, the more so when contrasted with the low self-fertility of the lines from selections from North Carolina Abruzzes. In 1922 the selfed

heads of the two selections from North Carolina Abruzzes produced only 7 seeds, as contrasted with 49 from the selfed plant (S2229) selected from Abruzzes C. I. 40–59. The second year of selfing of one plant from North Carolina Abruzzes gave 2 seeds as contrasted with 292 from 6 second-year selfs of S2229. The third year's selfing of two plants from the North Carolina Abruzzes gave no seed as contrasted with 591 from 19 third-year selfs of S2229. Even cross-pollinated material of the lines from North Carolina Abruzzes did not equal in seed production the selfs of S2229. Thus 40 cross-pollinated plants of North Carolina Abruzzes gave 724 seeds. Of these crosses 210 first-year selfs gave only 195 seeds, and 54 second-year selfs gave 11. Since the plants from both sources were grown under very similar conditions in the greenhouse, and were bagged in the same way, these results indicate a marked difference in self-fertility.

DISCUSSION

Resistance of rye to disease has been given relatively little attention. A few general field observations in Europe have been recorded. Sorauer (*8*) lists eight rye varieties as susceptible to "rust" in Germany and nine varieties as resistant. According to Vavilov (*11*), Jaczewski and Noviko noted differences in susceptibility of rye varieties to leaf rust, *Puccinia dispersa*. Eriksson (*2*) states that Petkus rye is resistant to snow-mold, while Zealand is susceptible.

In the United States, Mains and Leighty (*5*) studied, in the greenhouse, a number of varieties of rye for susceptibility to leaf rust (*Puccinia dispersa*). They found that all of the 68 varieties studied showed a great variation in susceptibility, individuals very highly resistant to leaf rust as well as those highly susceptible being found in all the varieties. Differences in susceptibility to stem rust (*Puccinia graminis secalis*), have been reported by Levine and Stakman (*3*), who find that the rye varieties Rosen, Swedish, and Prolific differ in their relative susceptibility to three strains of the rust. One of the strains of stem rust attached all three varieties heavily. Another attacked Rosen heavily, Prolific moderately, and Swedish weakly. The third strain produced normal infection on Swedish and Prolific, while only weakly infecting Rosen.

In the study on which this paper is based no attempt was made to investigate the susceptibility of a number of varieties or selections of rye to the three fungi used—leaf rust, stem rust, and powdery mildew. In connection with an investigation of leaf rust of rye, two selections made for resistance to leaf rust in Abruzzes rye from North Carolina, first attracted attention, for out of 69 such selections made from 12 varieties, these 2 proved also to be highly resistant to powdery mildew (*Erysiphe graminis secalis*). So far as the writer has been able to discover, resistance to powdery mildew has not previously been noted. In consequence, these two selections assumed greater importance than the rest. Since they possessed high resistance for two diseases, it seemed possible that they might also be resistant to others. This proved to be true when individuals resistant to stem rust were found to occur in their progenies. Consequently this material is outstanding in that it possesses resistance to three diseases, leaf rust, stem rust, and mildew, this resistance often occurring in the same individuals.

In attempting to obtain a line of rye from North Carolina Abruzzes pure for resistance to all three diseases, various difficulties were encountered. In the first place, the resistant rye plants, when selfed, produced little or no seed. In the second place, resistance to each of the three diseases apparently is inherited as a dominant character. As a result, when an attempt was made to purify for resistance by continued selfing of resistant selections, the lines were almost all lost through sterility. Crossing between resistant selections proved somewhat better. Even by this method, however, the number of seed produced, at best, was relatively few. Because of the dominance of resistance it was impossible to tell whether the plants crossed were homozygous or heterozygous for resistance. Selfs from such crosses in many cases produced susceptible as well as resistant plants, indicating that in these cases both parents probably were heterozygous. In those instances where the F_2 progeny of a cross between resistant individuals was entirely resistant, the number of individuals was so small that the possibility of heterozygosity is by no means eliminated. Further selfing resulted for the most part in loss of the line. In consequence, it has not been possible thus far to develop with certainty a line of rye from North Carolina Abruzzes pure for resistance to all three of the diseases studied.

As is shown by Tables I to IV, selfs of plants highly resistant to or almost immune from leaf rust, stem rust, and mildew, or crosses between such resistant plants, produced progenies in which classes of reaction occurred, ranging from nearly complete immunity through high resistance, moderate resistance, moderate susceptibility to high susceptibility. Individuals occurred intermediate in susceptibility, especially between the three classes of resistance, 0, 1, 2, and between the two classes of susceptibility, 3 and 4, so that in some cases it was necessary to place them more or less arbitrarily in one of two classes. This also complicates the situation and places another difficulty in the way to making a clear-cut interpretation of the data concerning inheritance of resistance.

This great variation in susceptibility of the progenies of resistant plants to each disease is in itself puzzling. It already has been noted by Mains and Leighty (*5*) for susceptibility of rye to leaf rust. For a somewhat similar range in the segregates for susceptibility to *Puccinia graminis* of a cross between resistant and susceptible varieties of wheat, Puttick (*7*) has suggested the existence of several genetic factors. Until lines of rye pure for resistance have been obtained, it is not possible to decide whether such is the explanation of the situation found in the rye studied.

As is shown by Table II, resistance to each of the three diseases is inherited independently of the others. This would indicate that whatever the factor or factors may be which determine resistance they are not the same for all three. In consequence, of the individuals showing resistance to all three diseases, those homozygous for resistance to all three are likely to be in relatively small number, which, taken with the large amount of sterility, makes it still more difficult to obtain a pure, disease-resistant strain.

It is apparent that self-sterility, so generally common in rye, is the greatest barrier to success in obtaining a strain homozygously resistant to the three diseases. That more or less self-fertile rye

can be obtained has been reported by Brewbaker (*1*). The lines of rye which have been derived from the S2229 selection of Abruzzes (C. I. 40–59) also have exhibited considerable self-fertility. Consequently, three generations of selfing and selection from a plant, originally heterozygous for leaf-rust susceptibility, has made it possible to isolate lines homozygous for leaf-rust resistance. A number of these lines, although they have been studied only for one generation for stem-rust and mildew resistance, are so uniformly resistant to both of these diseases that it is very probable that these lines of S2229 are also homozygous for resistance to the strains of stem rust and mildew employed.

It must be recognized however, that the development of a line of rye both self-fertile and homozygous for resistance to the three strains of the diseases which have been employed in this study, is only the beginning. Levine and Stakman (*3*) have found that there are at least two, and probably more, physiologic forms of the stem rust of rye. In the studies reported in this paper, only one strain of the stem rust of rye has been employed. It remains to be discovered whether this material is generally resistant to all forms of this rust. The same may hold true for the two other diseases, although there is no evidence of the existance of physiologic forms. However, a study of these diseases for the existance of such forms will be greatly facilitated by having, in each case, one or more homozygous resistant lines of rye and for that reason, if for no other, the development of such lines of rye is worth while.

SUMMARY

Plants highly resistant to leaf rust (*Puccinia dispersa*), stem rust (*Puccinia graminis secalis*), and mildew (*Erysiphe graminis secalis*), have been obtained from Abruzzes rye.

A study of two selections made from North Carolina Abruzzes indicates that resistance to each disease is dominant, selfs of resistant plants yielding progeny among which were individuals showing various degrees of susceptibility.

Resistance to each disease is inherited independently of the others, various combinations of resistance and susceptibility to the three diseases being found in the progeny, thus indicating that resistance to each disease is due to a separate factor or factors.

The combination of low self-fertility and dominance of resistance in the material derived from the North Carolina selections still leaves uncertain the purity of the selections obtained.

A selection (S2229) from Abruzzes C. I. 40–59, however, has yielded lines which have proved to be quite self-fertile through three generations of selfing.

From the selection S2229, a number of lines have been bred which are apparently homozygous for resistance to leaf rust.

A number of these have shown remarkable uniformity, and they show promise of being homozygous for resistance to stem rust and mildew as well as to leaf rust.

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WATER-CORE OF APPLES[1]

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INTRODUCTION

Water-core occurs in practically every important apple-growing section in the world. It has been described by writers from Europe, Africa, Australia, and America. Numerous observations have been reported as to the conditions that favor its occurrence, but apparently no extended investigation of the disease has ever been made. The opinion prevails that an excessive water supply is of first importance for the occurrence of the disease, and that excessive growth is also a contributing factor; but the studies of the present paper indicate that heavy irrigation tends to decrease water-core, that forcing with nitrate does not increase it, and that the real cause of the trouble is to be found in connection with high temperatures, intense sunlight, and the accompanying high sap concentration of the apples.

OCCURRENCE

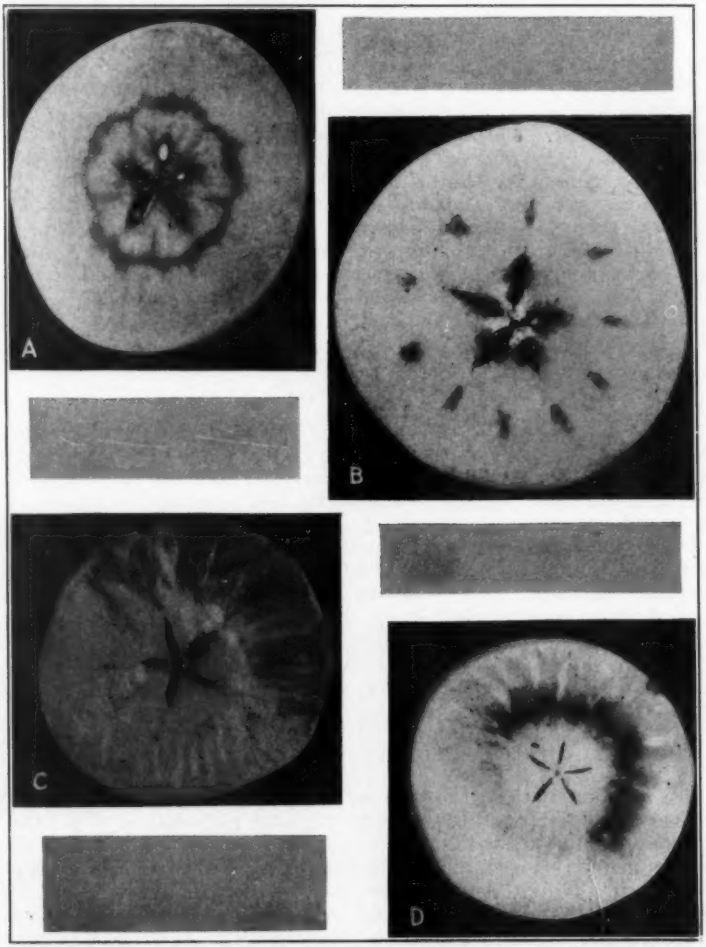
Water-core is erratic in occurrence, causing heavy losses in some seasons and almost none in others. It occurs in all of the apple-growing sections of the United States, but is most serious in the arid and semiarid regions where orchards are under irrigation and where intense sunlight prevails.

Early Harvest, Yellow Transparent, Pound Sweet, Fall Pippin, Tompkins King, Rambo, Winter Banana, Jonathan, Delicious, Stayman Winesap, and Winesap are among the varieties most susceptible to water-core. In the eastern part of the United States losses have been most severe on the summer and fall varieties. In the Northwestern States losses have been heaviest on varieties that are held on the tree for high color; for example, Jonathan, Delicious, Stayman Winesap, and Winesap.

CHARACTERISTICS OF THE DISEASE

The characteristic of water-core that sets it off from all other diseases of the apple is the watery or glassy appearance of the flesh of the apple, due to the filling of the intercellular spaces with water or cell sap instead of with air. Sometimes practically the whole apple is involved and the watery tissue is evident through the skin; but more often the disease is confined to the tissue bordering the vascular bundles, or that adjacent to the core (pl. 1, A, C). In the first stages of the disease there may be mere dots or streaks of water-core tissue scattered through the flesh. These are always associated with the vascular bundles, and may be around the larger bundles near the core or on the smaller divisions near the surface of the apple

[1] Received for publication June 30, 1925; issued February, 1926.



A.—Yellow Newtown apple, with bad water-core. Here the disease is confined largely to the region bordering the core

B.—Winesap apple, with water-core. Here is shown a mild form of the disease. Only the tissue immediately adjacent to the vascular bundles is affected

C.—Yellow Newtown apple, badly affected with water-core. The disease in this case is located in the sunburned half of the apple, with the core region remaining normal

D.—Yellow Newtown apple, which has partly recovered from water-core during storage. The darkest areas are still affected with the disease, while the more lightly shaded ones have an internal browning which has followed water-core

pl. 1, B). Water-core may start at a number of different points in the apple at approximately the same time, and the centers of origin may be widely separated by normal tissue. It is typically a disease of mature apples, yet it sometimes occurs several weeks before harvest.

HISTORICAL

Sorauer (*26, p. 142*)[2] apparently was the first to make a study of water-core of apples and to give a description of the disease. In his Handbuch der Pflanzenkrankheiten, published in 1886, he reported data showing that the dry weight of the water-core tissue in percentage of the fresh weight was lower than found in the normal tissue. He stated that trees were more disposed to the disease when young and first coming into bearing than they were in later years.

Cobb (*12*) apparently has given the first (1891) English description of the disease, reporting it as it was found in Australia. He reported the disease most abundant in moist seasons, and especially likely to appear after a long rain if this occurred near the time of harvest. He stated that the time at which the fruit begins to ripen is a period of rapid growth, and if the air is very moist, or if rain collects in the cavity at the stem end of the apple, the water apparently is absorbed, either through the stem or perhaps through the pip.

Arthur and Golden (*3, p. 61*) made passing reference to water-core in 1892, and Craig (*13, p. 173*) referred to it in 1896, which indicates that the disease has long been known in both the United States and Canada.

Aderhold (*2, p. 8–10*) found that water-cored tissue had a higher specific gravity and greater water content than normal tissue, but was lower in dry matter, ash, and malic acid.

Zschokke (*27, p. 195–196*) reported observations agreeing with the early studies of Sorauer and Aderhold.

Behrens (*5, p. 53*) found that partially water-cored tissue had a greater water content but less acid and invert sugar than the normal tissue.

McAlpine (*17, 18, p. 29; 19, p. 13*) reported that the disease was most common in wet years, especially if rains came about the time the apples began to ripen. He found large varieties with hard, firm flesh to be particularly susceptible to the disease, the early varieties more subject to it than the late ones, and the fruit from young trees more susceptible than the fruit from older ones.

Campbell (*9*) reported that the disease was more prevalent in moist districts and on poorly drained soils. He stated that "as the fruit matures a quantity of inefficient sap is passed in, and being unsuitable for use, and unable to escape, it water-logs the otherwise healthy cells."

Pole-Evans (*14*) stated that:

> Water-core * * * is undoubted evidence of water exudation under pressure. The cell sap fills the cells to overflowing, but instead of bursting them, quietly diffuses through their membranes or walls and then accumulates in the intercellular spaces. * * * Bitter-pit * * * results from the bursting * * * of certain cells of the flesh due to too great internal pressure. This great pressure is set up by the external conditions to which the trees are exposed.

[2] Reference is made by number (italic) to "Literature cited," p. 259.

Norton (*21*) reported the disease most abundant on summer and fall apples. He stated that:

> Apples near the top of the trees and on the sound part of branches that had been cut back by fire blight * * * were affected more than shaded apples or the slightly withered ones on the lower part of slightly blighted branches. * * * The occurrence of the disease under conditions favoring excessive sap pressure or cell turgor, on vigorous growing trees, or trees with the foliage reduced by blight, and especially in late summer when the air is cold at night and the soil warm, the cracks in the carpels, the occurrence along the vascular tissue, the liquid filling the intercellular spaces, lead me to the conclusion that the trouble is due to sap forced into the seed cavities and intercellular spaces by excessive sap pressure under conditions of reduced transpiration.

He also suggested that the rapid conversion of starch into sugar in the ripening processes of the fruit might have a bearing on the occurrence of the disease.

Bothe (*7*) noted that water-core had been particularly bad in certain years when the apples ripened much earlier than usual. He believed that excessive heat played a part in the production of the disease.

O'Gara (*22*, *23*) reported that excessive soil moisture shortly before the maturity of the fruit, if followed by extremes of temperature and atmospheric humidity, was a factor of the greatest importance in producing water-core. He found the disease worst on the south and southwest parts of the trees, and that slightly water-cored fruit largely recovered from the trouble when held in cool (not cold) storage.

Clinton (*11*, *p. 8*) thought that the unusual prevalence of water-core in Connecticut in 1913 was due to the very wet weather in October of that year, and possibly to the rapid growth of the fruit after the June–July drought.

Ramsey, McKay, Markell, and Bird (*24*) reported that water-cored King David and Tompkins King apples should not be stored, as they usually decayed early in storage. The varieties with a firm flesh, like the Winesap and Yellow Newtown, behaved much better in storage, but the water-cored apples could not be held as long as sound ones.

Hesler and Whetzel (*15*) have given a very complete summary of water-core information in their "Manual of Fruit Diseases."

Rivière and Pichard (*25*) reported comparative analyses on the two halves of a White Caville apple, one side of which was water-cored. They found that the affected part of the apple had less saccharose and less glucose than the sound part. They thought that sugars disappeared under the action of anaerobic fermentation, the acidity remaining essentially the same.

Lewis (*16*) noted that excessive thinning of Rome Beauty apples tended to aggravate water-core.

Ballard, Magness, and Hawkins (*4*, *p. 17*) found that the girdling of branches resulted in a tendency to water-core in the apples.

Birmingham (*6*) reported that water-core was probably due to heavy rains, heavy pruning, and late picking.

Adams (*1*) reported that the disease was apparently associated with several days of continuous rain just before harvest.

IRRIGATION EXPERIMENTS

A study of the literature shows a preponderance of opinion that heavy rainfall and excessive soil moisture are largely responsible for the development of the disease, and the writers deemed it desirable to test this point by irrigation experiments.

The experiments were located at Wenatchee, Wash. They were carried out in a manner similar to those reported in an earlier publication (*8*). The amount of water in the soil was determined from samples taken with a soil auger. From 200 to 300 grams of soil were in each sample. The sample was weighed, then the soil was reduced to constant weight in a drying oven at a temperature of approximately 100° C., and then was weighed again. The difference between the two weighings was taken as the moisture content of the sample, and the percentage of moisture was determined by comparing this moisture content with the dry weight of the sample.

In a part of the experiments a record was also kept of leaf moisture and evaporation conditions. The relative evaporation in the different plots was determined by means of Livingston atmometers suspended at different points in the trees. The spheres were standardized before use, and care was taken that their surfaces should not be touched, but dust and leaf hoppers made it impossible to keep them clean and necessitated frequent replacement where records were made over a long period. In the leaf-moisture studies samples consisting of 100 square centimeters were cut from the leaves of the different plots with a Ganong leaf-area cutter, care being taken to avoid the midribs and larger veins. The samples were transferred at once to small vials. They were weighed, then dried to constant weight before an electric heater at a temperature of approximately 90° C., and then weighed again to determine the loss of water.

IRRIGATION EXPERIMENTS IN 1919

The 1919 experiments were made on the Winesap and Yellow Newtown varieties. The trees were 16 years old, well grown, and very thrifty. They had received a heavy application of "complete fertilizer" in the spring, and alfalfa had been grown as a cover crop for two years prior to the starting of the experiment. The soil was a Cashmere sandy loam, somewhat stony in the Winesap orchard, but free from stones in the Yellow Newtown orchard.

The different plots were irrigated alike until the middle of July. Soil samples were taken weekly after July 7. The soil-moisture conditions for the season are shown in Figures 1 and 2. Plots 2 and 3 of the Winesap experiment received more water in August than was intended. Plot 3 should have had heavy irrigation after September 10, but the water was not available and it thus became practically a duplicate of plot 2. The Yellow Newtown irrigations were carried out practically as planned, with the exception that plot 4 did not dry out as fast as expected. It was heavily irrigated in July and August, but received no water after September 10.

A study of the figures shows that there was a distinct contrast between the soil-moisture conditions in the heavily and lightly irrigated Winesap plots, and a very decided contrast in the Yellow Newtown plots.

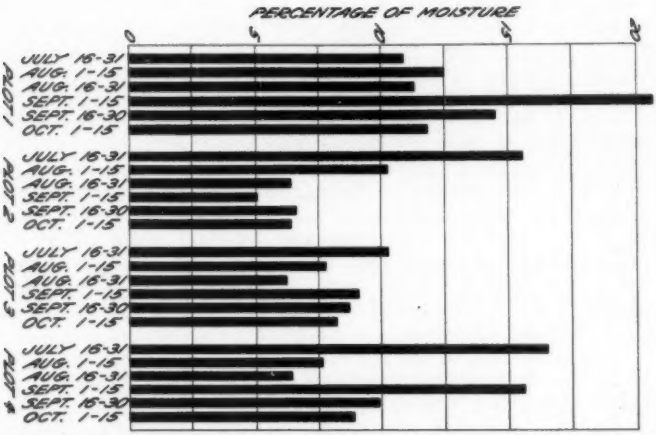


FIG. 1.—Showing the soil-moisture conditions in the irrigated plots of Winesap in 1919. The bars show the average percentage of moisture for each half month, based on the dry weight of soil samples at depths of 18 and 36 inches. Plot 1 received heavy irrigation throughout the season; plot 2, light irrigation; plot 3, light irrigation (should have been heavy after September 10); and plot 4, heavy irrigation, with 4 pounds of nitrate of soda applied per tree in the irrigation furrows on July 20

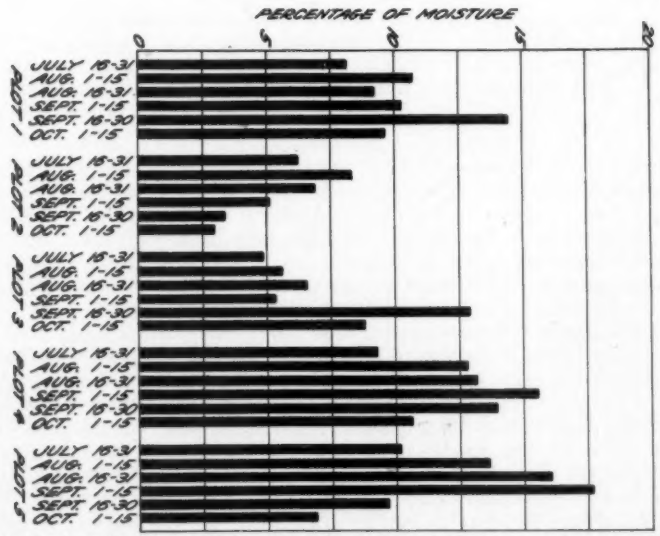


FIG. 2.—Showing soil-moisture conditions in the irrigated plots of Yellow Newtown in 1919. The bars show the average percentage of moisture for each half month, based on the dry weight of soil samples at depths of 18 and 36 inches. Plot 1 received heavy irrigation throughout the season; plot 2, light irrigation; plot 3 light irrigation until Sept. 10, then heavy irrigation; plot 4, heavy irrigation throughout the season, with the addition of 8 pounds of nitrate of soda per tree; and plot 5 heavy irrigation until September 10, then no irrigation

TABLE I.—*Evaporation in the Yellow Newtown irrigation plots, 1919*

Period of record and location of the atmometer	Evaporation ratio, cubic centimeters evaporated per atmometer	
	Heavy irrigation	Light irrigation
Period of Aug. 23 to 30, 1919:		
Atmometer in top of tree	172.5	188.0
Atmometer on lower south side of tree	148.5	170.5
Atmometer on lower north side of tree	148.5	157.0
Average for the above three atmometers during the following periods:		
7 p. m. Aug. 23 to 7 a. m. Aug. 24	7.6	7.5
7 a. m. to 7 p. m. Aug. 25	11.0	13.8
7 p. m. Aug. 25 to 7 a. m. Aug. 26	16.5	17.3
7 a. m. to 7 p. m. Aug. 26	16.7	19.3
7 p. m. Aug. 26 to 7 a. m. Aug. 27	13.3	14.8
7 a. m. to 7 p. m. Aug. 27	17.0	21.7

TABLE II.—*Percentage of moisture in Yellow Newtown leaves, irrigation experiments of 1919 (each record is based on approximately 100 square centimeters of leaf area)*

Time of collecting	Location of leaves	Percentage of moisture based on dry weight of leaf tissue	
		Heavy irrigation	Light irrigation
3.30 p. m. Aug. 27	Top of tree	146.0	121.0
Do	Lower south side	141.5	127.1
Do	Lower north side	145.5	
7.30 p. m. Aug. 27	Top of tree	173.5	141.9
Do	Lower south side	118.0	126.8
Do	Lower north side	151.3	143.8
9 a. m. Aug. 28	Top of tree	173.5	134.2
Do	Lower south side	135.3	132.6
Do	Lower north side	157.8	127.8

The evaporation and leaf-moisture conditions in the heavily irrigated and the lightly irrigated Yellow Newtown plots are shown in Tables I and II. The irrigation effects were evident in the foliage and the surrounding air as well as in the soil-moisture conditions. The leaves from the heavily irrigated plot were surrounded by a more humid atmosphere and had a higher percentage of moisture than those of the lightly irrigated plot. There was no contrast, however, in the general appearance of the foliage or the fruit of the different plots.

On July 20, 4 pounds of nitrate of soda were applied to each tree in plot 4. The fertilizer was applied in the furrows and worked in with the irrigation water.

The Winesap apples were picked October 24, and the Yellow Newtown October 28. Heavy freezes occurred on the nights of October 25 and 26 and the Yellow Newtown were frozen to the core. Picking was delayed until the apples had thawed, and no damage was evident. Plots 1 and 4 of the Winesap experiment had heavier crops than Plots 2 and 3, but in the Yellow Newtown experiment the fruit was evenly distributed over the different plots.

TABLE III.—*Effect of irrigation and fertilizers upon the size of apples (Winesap and Yellow Newtown experiments, 1919)*

Variety, plot, and treatment	Percentage of apples of the following size			
	2¾ inches or less	2¾ to 3 inches	3 to 3¼ inches	3¼ to 3½ inches
Winesap:				
Plot 1, heavy irrigation	59.5	30.4	9.1	1.0
Plot 2, light irrigation	26.2	50.5	20.4	2.9
Plot 3, light irrigation	24.9	45.0	25.3	4.8
Plot 4, heavy irrigation, with sodium nitrate	66.5	25.5	6.1	1.9
Yellow Newtown:				
Plot 1, heavy irrigation	24.3	30.7	26.6	18.4
Plot 2, light irrigation	48.8	29.4	17.8	10.0
Plot 3, light irrigation followed by heavy	33.1	34.1	20.3	12.5
Plot 4, heavy irrigation, with sodium nitrate	33.1	37.6	21.1	8.2
Plot 5, heavy irrigation, followed by light	29.1	30.3	27.9	12.7

The apples from the different plots were graded according to size, with the results shown in Table III. Plots 1 and 4 of the Winesap had a relatively large percentage of the smallest size (2¾-inch or smaller), probably due to the result of heavy crop on these plots; while plots 1 and 5 of the Yellow Newtown had a relatively small percentage of this size.

There was no water-core visible on the Winesap at picking time, and only a little on the Yellow Newtown. From 2 to 6 boxes of apples were saved from each plot and placed in cellar storage. Approximately half of these were cut on November 12 and the percentage of water-core determined. The results are shown in Table IV.

TABLE IV.—*Effect of irrigation upon water-core (Winesap and Yellow Newtown apples; notes taken November 12, 1919)*

Variety, plot, and treatment	Percentage of water-core				
	2¾ inches or less	2¾ to 3 inches	3 to 3¼ inches	3¼ to 3½ inches	Total all sizes
Winesap:					
1. Heavy irrigation	36.1	85.6	61.4	60.0	46.3
2. Light irrigation	40.7	71.1	81.0	100.0	73.8
3. Light irrigation	66.7	81.5	77.5	91.0	77.4
4. Heavy irrigation, with sodium nitrate	50.1	67.6	71.9	40.0	55.7
Yellow Newtown:					
1. Heavy irrigation	7.8	17.8	29.0	46.9	23.7
2. Light irrigation	10.4	26.2	46.0	62.8	36.7
3. Light irrigation till Sept. 10, then heavy	7.4	13.9	30.8	54.5	20.3
4. Heavy irrigation, with sodium nitrate	7.3	25.3	29.2	36.4	21.1
5. Heavy irrigation till Sept. 10, then none	7.5	26.1	36.2	50.0	26.5

There was more water-core in the lightly irrigated apples than in the heavily irrigated ones, and there was more where heavy irrigation was followed by light than where light was followed by heavy. The fertilizer results are discussed on page 239.

IRRIGATION EXPERIMENTS IN 1920

The irrigation experiments on Winesap were continued in 1920, but in a different orchard from that used in 1919. The trees were 8 years old, well pruned, and well cared for generally. They had made an average terminal growth of 2 feet the previous season. The soil was Cashmere sandy loam and was very uniform and very retentive of moisture. The orchard was in alfalfa and had been continuously for three years previous,

The irrigations were carried out more satisfactorily than in the previous year. The soil-moisture conditions are shown in Figure 3. It will be seen that there was a very marked contrast between the two plots, the one receiving heavy irrigation having from 7 to 10 per cent of moisture continuously after the middle of July, while the one that received light irrigation had 6.5 per cent in July, 5 per cent in August, and 3 to 4 per cent in September and October.

TABLE V.—*Evaporation in the Winesap irrigation plots, July 19 to September 18, 1920*

Period of record	Evaporation ratio, cubic centimeters evaporated per atmometer			
	In top of tree		In crotch of tree	
	Heavy irrigation	Light irrigation	Heavy irrigation	Light irrigation
July 19 to July 27	42.94	42.32	39.55	39.62
July 27 to Aug. 4	32.54	36.03	31.55	34.21
Aug. 4 to Aug. 12	24.12	27.60	23.28	26.32
Aug. 12 to Aug. 19	26.52	29.46	24.60	28.70
Aug. 19 to Aug. 26	17.29	19.92	16.12	18.73
Aug. 26 to Sept. 2	12.36	13.20	11.20	13.99
Sept. 2 to Sept. 11	17.78	20.16	18.10	19.55
Sept. 11 to Sept. 18	11.04	12.18	10.04	11.91

A record was kept of leaf moisture and evaporation under the different irrigation conditions. The evaporation data are reported in Table V. As in the 1919 experiment, the rate of evaporation was decidedly higher in the lightly irrigated plot than in the heavily irrigated one. It was also higher in the top of the tree than in the region of the lower limbs. Seven leaf-moisture tests were made in August, three in September, and two in October, but, contrary to results of the preceding year, the data showed practically no contrast between the foliage of the heavily irrigated trees and that of the lightly irrigated ones.

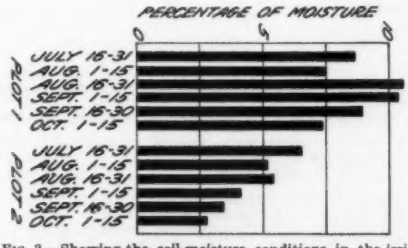


FIG. 3.—Showing the soil-moisture conditions in the irrigated plots of Winesap in 1920. The bars show the average percentage of moisture for each half month, based on the dry weight of soil samples at depths of 18 and 36 inches. Plot 1 received heavy irrigation, and plot 2 light irrigation, throughout the season

The weather was cool and cloudy during the last week of August and the first week of September and was accompanied by a strong development of color on the fruit. The apples of plot 2 took on a higher color than those of plot 1. The apples in both plots increased in diameter rapidly throughout the latter part of the season up to October 8 and at a slower rate after that until October 25, when the fruit was picked. (See fig. 8.) No contrast was evident in the foliage of the different plots, and there was but little difference in the percentages of apples of the different sizes. (See Table VI.)

TABLE VI.—*Effect of irrigation upon the size of the apples (Winesap experiments, 1920)*

Plot and treatment	Percentage of apples of the following sizes			
	2¾ inches or less	2¾ to 3 inches	3 to 3¼ inches	3¼ to 3½ inches
1. Heavy irrigation	33.4	40.5	20.6	5.5
2. Light irrigation	37.2	42.7	19.4	0.7
3. Regular orchard irrigation	43.9	35.7	16.8	3.6

The picked fruit was stored in air-cooled and cellar storage till November 26 and 27, when the apples were cut open and notes taken on water-core. The results are shown in Table VII.

TABLE VII.—*Effect of irrigation upon water-core (Winesap apples; notes taken November 26 and 27, 1920)*

Plot and treatment	Percentage of water-core				
	2¾ inches or less	2¾ to 3 inches	3 to 3¼ inches	3¼ to 3½ inches	Total all sizes
1. Heavy irrigation	31.6	48.0	67.6	70.3	47.8
2. Light irrigation	81.7	97.7	100	100	92.2
3. Regular orchard irrigation	51.7	93.7	100	100	79.2

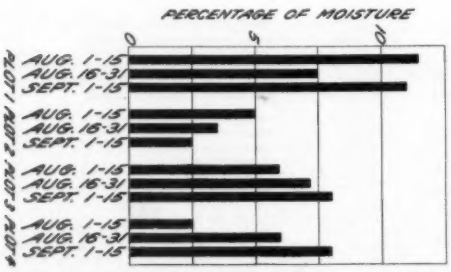


FIG. 4.—Showing the soil-moisture conditions in the irrigated plots of Winesap in 1921. The bars show the percentage of moisture, based on the dry weight of the soil. The results are the average of samples taken from depths of 18 and 36 inches. Plot 1 received heavy irrigation throughout the season, and plot 2 received no irrigation after June 27

The apples from the lightly irrigated trees had nearly twice as much water-core as those from the heavily irrigated ones. The apples from plot 3 receiving the regular orchard irrigation, which was medium as compared with the other plots, also had a very much higher percentage of water-core than the apples from the heavily irrigated trees.

IRRIGATION EXPERIMENTS IN 1921

The experiments were continued in the orchard used in 1920, but on trees that had not been included in the previous plots. Owing to a shortage of help, the irrigation work was not carried out as carefully nor were the soil samples taken as frequently as in previous years. The approximate soil-moisture conditions for August and the first half of September are shown in Figure 4. The dry plot received no water after June 27, while the others received frequent irrigations throughout the remainder of the season. On August 31,

there was a decided contrast between the wet and dry plots, as evidenced by the smaller size of the leaves and sparser foliage on the lightly irrigated trees. Plot 1 was given a heavy irrigation at this time and another irrigation on September 16. It is believed that the soil-moisture contrasts shown in Figure 4 were maintained till the apples were picked.

Red spiders and leaf hoppers were bad throughout the orchard, causing considerable foliage injury.

On July 14, 7½ pounds of nitrate of soda were applied to each tree in plot 3, and 7½ pounds muriate of potash to each tree in plot 4. The fertilizers were applied in the furrows and worked in with the irrigation water.

The fruit was picked on October 13, and held in the shade in the open till October 29, when the apples were cut open and notes taken on water-core. The results are shown in Table VIII.

TABLE VIII.—*Effect of irrigation upon the development of water-core (Winesap apples in 1921; notes taken October 29)*

Plot and treatment	Percentage of water-core		
	Bad	Slight	Total
1. Heavy irrigation	3	38	41
2. Light irrigation	8	29	37
3. Medium irrigation, with nitrate of soda	1	6	7
4. Medium irrigation, with muriate of potash	1	15	16

The lightly irrigated apples had more bad water-core but less slight water-core than the heavily irrigated ones. The total percentage of the disease was slightly greater on the heavily irrigated apples. Plots 3 and 4 with medium irrigation and applications of fertilizers had the least water-core. (For discussion of fertilizers see p. 239.)

IRRIGATION EXPERIMENTS IN 1922

The work was continued in the Winesap orchard used in 1920 and 1921. The irrigations were carried out as planned and the contrasts in soil moisture were very satisfactory. Soil samples were taken every week at 18-inch and 36-inch depths. The results are shown in Figure 5.

On June 17, 5 pounds of nitrate of soda were applied to each tree in plots 5 and 6 and 5 pounds of muriate of potash to each tree in plots 7 and 8. The trees of plot 5 were included in the nitrate plot, and those of plot 7 in the potash plot of the 1921 experiment.

The growth conditions were good in all of the plots throughout the year and no contrast was evident in foliage or fruit. The apples were picked October 24, with a yield of approximately 8 bushels per tree. The apples remained in the shade in the orchard till November 4, when they were graded for size, and from two to three boxes of apples from each plot cut open and examined for water-core. The remainder of the apples was placed in cellar storage and a second record made on November 23. The percentage of apples of the different sizes from the various plots is shown in Table IX and the water-core results in Table X.

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TABLE IX.—*The effect of irrigation and fertilizers upon the size of the apples (Winesap experiment, 1922)*

Treatment	Percentage of apples of the following sizes:			
	2¼ inches or less	2¼ to 3 inches	3 to 3¼ inches	3¼ to 3½ inches
1. Heavy irrigation	49.3	40.6	8.8	1.3
2. Light irrigation	47.0	43.0	9.1	.9
3. Light irrigation followed by heavy	38.8	44.3	15.3	1.6
4. Heavy irrigation followed by light	63.1	30.0	6.9	.0
5. Nitrate of soda in 1921 and 1922	11.4	55.3	30.8	3.5
6. Nitrate of soda in 1922 only	26.1	56.4	16.1	1.4
7. Muriate of potash in 1921 and 1922	30.5	41.0	22.3	6.2
8. Muriate of potash in 1922 only	42.1	50.5	6.4	1.0

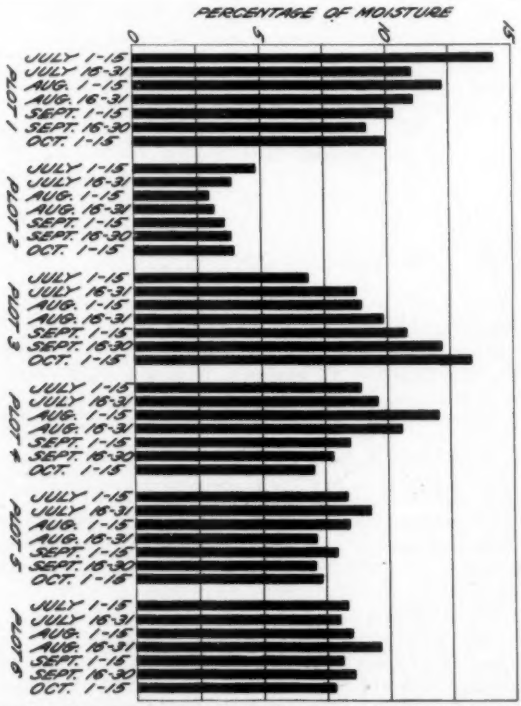

FIG. 5.—Showing the soil-moisture conditions in the Winesap irrigation plots of 1922. The bars show the average percentage of moisture, based on the dry weight of soil samples taken from depths of 18 and 36 inches. Plot 1 received heavy irrigation throughout the year; plot 2, light irrigation; plot 3, light irrigation until Aug. 20, then heavy; plot 4, heavy irrigation until Aug. 20, then light; and plots 5 and 6, medium to heavy irrigation, and an application of nitrate of soda

The percentages of apples of the different sizes were approximately the same on the heavily and lightly irrigated plots. With those receiving heavy irrigation followed by light there was a relatively large number in the smaller or 2¾-inch size; and with those receiving light irrigation followed by heavy, and also with the fruit from the nitrate plots there was a relatively large number in the larger sizes.

TABLE X.—*The effect of irrigation and fertilizer upon the development of water-core (Winesap apples in 1922)*

Plot, treatment, and date of note taking. (For degree of irrigation see fig. 5)	Percentage of water-core in the following sizes:				
	2¾ inches or less	2¾ to 3 inches	3 to 3½ inches	3¼ to 3½ inches	Total, all sizes
Notes of Nov. 4:					
Plot 1, heavy irrigation (heavy irrigation the previous year)	74.0	82.5	87.9	87.7	81.9
Plot 2, light irrigation (light irrigation the previousyear)	74.9	82.4	100.0	----------	78.6
Plot 3, light irrigation till Aug. 20, then heavy (not treated in previous experiments)	38.3	57.1	86.7	100.0	49.2
Plot 4, heavy irrigation till Aug. 20, then light (not treated in previous experiments)	67.2	82.4	84.6	----------	76.5
Plot 5, nitrate of soda in 1921 and 1922	87.5	94.8	98.4	100.0	95.6
Plot 6, nitrate of soda in 1922 only	95.2	98.6	100.0	100.0	98.0
Plot 7, muriate of potash in 1921 and 1922	86.2	92.7	96.2	100.0	93.0
Plot 8, muriate of potash in 1922 only	94.0	92.4	94.1	94.3	93.2
Notes of Nov. 23:					
Plot 1	43.2	53.9	90.5	100.0	53.1
Plot 2	85.7	81.9	88.4	80.0	84.4

The apples that received light irrigation followed by heavy had less water-core than those that received heavy irrigation followed by light. If the records of both November 4 and 23 are considered, the apples from trees receiving continuous heavy irrigation after July 1 had decidedly less water-core than those from trees receiving light irrigation during the same period. (For discussion of size of fruit and effect of fertilizers, see pp. 239 and 241.)

IRRIGATION EXPERIMENTS IN 1923

The experiments were carried out in a 12-year old Winesap orchard. The trees were uniform and in excellent vegetative condition. An alfalfa cover crop had been maintained for the two years previous. The orchard had a gentle slope both lengthwise of the rows and diagonally across them. The soil was of the Quincy fine sandy loam type, underlaid at a depth of about 30 inches by a rather heavy clay loam that became still heavier at a depth of 36 inches. At 48 inches gravel was found in all the plots, with the exception of plot 2, and in this a sticky gray clay was found at the 4-foot depth.

Irrigation was begun by the grower on May 7. Each irrigation was continued 3 days before the water was changed, and the interval between irrigations was 13 days. The special irrigations for the water-core experiments were begun the last of July, and the soil-moisture conditions for the remainder of the season are shown in Figure 6. It was found soon after the experiment was started that the dry plots were being subirrigated from the more heavily irrigated ones higher on the slope. The upper row of the dry plot was disregarded thereafter in the experiment and was considered as a buffer row, and all of the soil and fruit samples were taken from the lower row. Even with this precaution there was little contrast between the soil-moisture conditions in the wet and dry plots at the 36-inch depth. Heavy rains the last of September and the first of October also interfered with the irrigation plans. Plot 3 was intended to be dry after August but it did not dry out much. In spite of these various difficulties, it will be seen from Figure 8 that a fair contrast was maintained between the soil-moisture conditions

in the wet and those in the dry plot at the 18-inch depth, and the sap-concentration studies reported later (Table XX) furnish evidence that the irrigation effects actually reached the foliage and fruit.

The soil temperature in the different plots and under different orchard conditions was taken at intervals throughout the season, readings being taken from a depth of about 4 inches. The results are shown in Table XI. The soil in the dry plot was sometimes a few degrees warmer than that in the wet plot. The clean-cultivated soil was warmer than that in alfalfa.

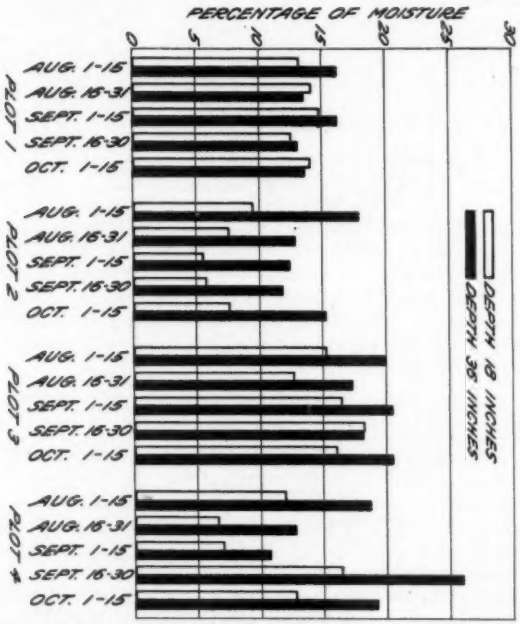

FIG. 6.—Showing the soil-moisture conditions in the irrigated plots of Winesap in 1923. The bars show the percentage of moisture, based on the dry weight of samples taken from depths of 18 and 36 inches. Plot 1 received heavy irrigation after July; plot 2, light irrigation; plot 3 was intended to have heavy irrigation followed by light; and plot 4 received light irrigation from July 27 to September 14, then heavy irrigation

TABLE XI.—*Soil and air temperature in the Winesap plots, 1923*

Date	Hour	Air temperature	Soil temperature						
			Plot 1	Plot 2	Plot 3	Plot 4	Clean cultivation	8-year alfalfa	2-year alfalfa
July 27	10 a. m.	86		71			74	68	
Aug. 4	do.	72	63	66					
Do.	10.30 a. m.	85					74	68	68
Aug. 27	10.00 a. m.	79	69	69	68	72	78	68	70
Sept. 10	3 p. m.	88	67	70	75				
Sept. 17	2.30 p. m.	85	63	67	68	73	65	62	
Oct. 1	10.00 a. m.	59	57						
Oct. 7	do.	70	60						
Oct. 21	do.	58	47						

During August considerable leaf injury became evident. This probably was a result of spraying. The edges of the leaves were scorched, and some defoliation occurred.

On October 16 it was noticed that the apples were beginning to drop badly throughout the orchard and were apparently ripe, but the experimental plots were not picked until October 21. The fruit was held in air-cooled storage until October 31, when half of the apples from each lot were cut open and examined for water-core. The results are shown in Table XII.

TABLE XII.—*The effect of irrigation upon the development of water-core (Winesap experiment, 1923)*

Plot and treatment	Percentage of water-core		
	Slight	Bad	Total
1. Heavy irrigation after July	56.1	1.4	57.5
2. Light irrigation after July	64.6	2.5	67.1
3. Heavy irrigation in July and August; no water after Aug. 31	53.7	28.8	82.5
4. Light irrigation to Sept. 14, followed by heavy irrigation	79.4	8.8	88.2

The lightly irrigated apples had more water-core than the heavily irrigated ones, and those that were heavily irrigated during July and August, with no irrigation in September or October, had the most bad water-core of all, but not as high total percentage of water-core as the apples from plot 4 which received light irrigation followed by heavy.

IRRIGATION EXPERIMENTS IN 1924

The experiments were carried out in an 18-year-old King David orchard. The trees had been well cared for and were in a good growing condition. The soil was Quincy fine sand with a loamy texture. Soil samples were taken every week at 18-inch and 36-inch depths. The soil-moisture conditions of the season are shown in Figure 7.

The soil-moisture in plot 2 was much lower during the latter part of the season than that of plots 1 and 3, and the foliage of the plot showed some tendency to wilt on extremely hot days, but there was no indication that the trees of this plot were really suffering from drought. Leaf-moisture tests based on the dry weight of whole leaf material collected September 3 gave 93.8 per cent of moisture in the leaves from the heavily irrigated plot and 86.4 per cent in the leaves from the lightly irrigated plot.

On June 3, 5 pounds of nitrate of soda were applied to each tree in plot 3.

The main commercial picking of the orchard was made September 5 and 6. At this time a bushel sample of apples was taken from the exposed top on the south side and another from the shaded interior of each count tree. The apples were held in basement storage at a temperature of about 70° until September 16, when they were graded according to size and cut open for notes on water-core. There was no water-core on the apples from the shaded interior of the trees. The results on the exposed apples are shown in Tables XIII and XIV.

TABLE XIII.—*Effect of irrigation and fertilizer upon the size of King David apples, 1924*

Treatment	Percentage of apples of the following sizes			
	2¾ inches or less	2¾ to 3 inches	3 to 3¼ inches	3¼ to 3½ inches
Picked Sept. 5 and 6:				
Plot 1, heavy irrigation	80	19	1	0
Plot 2, light irrigation	76	17	6	1
Plot 3, heavy irrigation, with sodium nitrate	79	19	2	0
Picked Sept. 25:				
Plot 1, heavy irrigation	67	30	3	0
Plot 2, light irrigation	61	38	1	0
Plot 3, heavy irrigation, with sodium nitrate	54	41	5	0

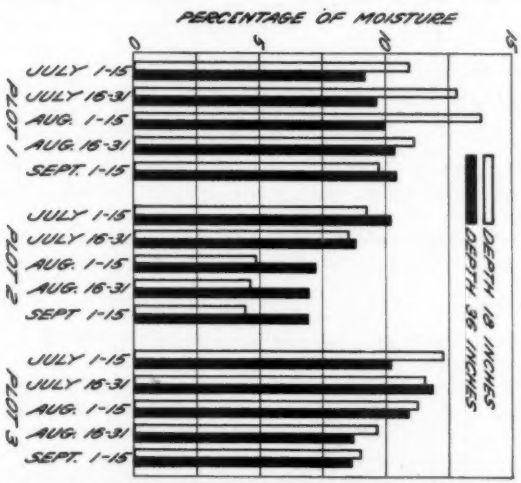

FIG. 7.—Showing the soil-moisture conditions in the King David irrigation plots of 1924. The bars show the percentage of moisture for each half month, based on soil samples taken at depths of 18 and 36 inches. Plot 1 received heavy irrigation throughout the season; plot 2, light irrigation; and plot 3, heavy irrigation, with five pounds of sodium nitrate per tree (spaded into the irrigation furrows) on June 3

TABLE XIV.—*Effect of irrigation upon water-core (King David apples, 1924)*

Plot and treatment	Percentage of water-core in apples of the following sizes			
	2¾ inches or less	2¾ to 3 inches	3 to 3¼ inches	Total, all sizes
Picked Sept. 5 and 6:				
Plot 1, heavy irrigation	0.9	0	0	0.7
Plot 2, light irrigation	.5	0	0	.4
Plot 3, heavy irrigation, with sodium nitrate	1.0	0	0	.8
Picked Sept. 25:				
Plot 1, heavy irrigation	56.8	89.5	100.0	82.7
Plot 2, light irrigation	80.0	100.0	100.0	87.8
Plot 3, heavy irrigation, with sodium nitrate	46.8	75.0	100.0	61.0

At the time of the regular picking, an upper branch with southern exposure was left unpicked on one tree of each plot, to determine the later development of water-core. The apples from these branches were picked September 25. At that time they had a deep-red color and were beginning to soften. Notes on the size of the apples and on the percentage of water-core were taken September 27. The results are shown in Tables XIII and XIV.

With the picking of September 5 and 6 the small apples had a higher percentage of water-core than the large ones, and the heavily irrigated apples a higher percentage than the lightly irrigated ones, but as no lot had more than 1 per cent of the apples affected it would seem that little weight should be given to the results.

By the time of the September 25 picking, more than three-fourths of the apples had developed water-core. The lightly irrigated apples had a higher percentage affected than the heavily irrigated ones, and the large apples a decidedly higher percentage of the disease than the small ones.

SUMMARY OF IRRIGATION EXPERIMENTS

The irrigation experiments cover a period of six years with 5 separate tests on Winesap, 1 on Yellow Newtown, and 1 on King David. In all of the experiments except one, where the percentage of the disease was large enough to be significant, the lightly irrigated fruit had more water-core than the heavily irrigated and in most cases the contrast was decided. The exception was in the case of the Winesap experiment of 1921, where 37 per cent of the lightly irrigated apples and 41 per cent of the heavily irrigated ones were affected with water-core. It has already been pointed out that the irrigation plans were not carried out as satisfactorily in this experiment as they were in the others, and it is probable that this fact accounts for the failure to obtain similar results.

In the 1919 experiments on Yellow Newtown and the 1922 experiments on Winesap, the apples that received heavy irrigation followed by light had more water-core than those that received light irrigation followed by heavy. In the 1923 experiments on Winesap, the apples receiving heavy irrigation followed by light had more bad water-core but less total water-core than those that received light irrigation followed by heavy.

The results as a whole give no indication that a sudden excess of soil moisture is a factor in the production of water-core, but, on the contrary, show that a liberal supply of water tends to make the fruit less susceptible to the disease, and this apparently holds for the latter part of the season as well as earlier in the year.

FERTILIZER EXPERIMENTS

Fertilizer experiments carried out on Yellow Newtown in 1919, on Winesap in 1919, 1921, and 1922, and on King David in 1924 have been reported in connection with the irrigation data in Tables IV, VII, X, and XIV. Similar tests were made on Jonathan in 1921, 1922, 1923, and 1924. In all of these experiments the fertilizer was worked into the soil in the bottom of the irrigation furrow, giving opportunity for it to pass rapidly into the soil solution. High-grade commercial nitrate of soda and muriate of potash were used in all cases.

The Jonathan tests were made on trees that were 14 years old at the beginning of the experiment. The soil was Wenatchee fine sandy loam. In 1921 the fertilizer was applied on July 16, in 1922 on June 6, in 1923 on July 9, and in 1924 on June 9. In 1921, 7½ pounds of nitrate of soda was applied to each tree in the nitrate plot, and 7½ pounds of muriate of potash to each tree in the potash plot. In 1922 the applications were reduced to 5 pounds per tree. In 1923 the nitrate application consisted of 5 pounds per tree, and the potash 3½ pounds per tree; and in 1924 the nitrate application was 5 pounds per tree, and the potash 6 pounds per tree.

The trees that were continued in the nitrate plot a second year had a somewhat darker green and heavier foliage than the other trees and produced apples with less color, but the potash fertilizers had no effect upon the general appearance of the foliage and fruit even after applications in four consecutive years. The terminal growth was greater on the fertilized trees than on the unfertilized ones. Measurements taken October 9, 1924, showed that the terminal growth in untreated trees averaged 13.2 centimeters; that in trees which had received nitrate one year, three years, and four years averaged 13.1, 20.2, and 24.2 centimeters, respectively; and that in trees which had received potash one year, three years, and four years averaged 17.2, 13.8, and 19.4 centimeters, respectively. It was found at picking time that the trees of the nitrate and potash plots had a slightly higher percentage of apples of the larger sizes than the untreated trees.

TABLE XV.—*Effect of nitrate of soda and muriate of potash upon the development of water-core in Jonathan apples*

Year and treatment	Percentage of water-core		
	Nitrate	Potash	No fertilizer
1921, apples picked Oct. 15;[a] notes taken Oct. 22	53.7	43.5	84.7
1922, apples picked Sept. 22; notes taken Oct. 25:			
Fertilizer in 1922 only	22.9	38.3	47.4
Fertilizer in 1921 and 1922	18.8	36.1	
1923, apples picked Sept. 14	8.6	6.2	20.3
1923, apples picked Oct. 5[a]	34.6	71.8	47.2
1924, apples picked Sept. 6; notes taken Sept. 17:			
Fertilizer in 1924 only	4.6	4.0	16.3
Fertilizer in 1921, 1922, 1923, and 1924	2.8	0.8	

[a] Apples picked in October were past their best commercial stage.

The effects of the various fertilizer treatments upon water-core are shown in Table XV. It will be seen that in every instance the apples from the nitrate plots had less water-core than those from the unfertilized plots, and in every instance except one the apples from the potash plots also had less of the disease than the apples from the untreated plots.

The results of the fertilizer tests on Yellow Newtown and King David apples reported in Tables IV and XIV are in agreement with those on Jonathan. Water-core was decreased on both varieties by the use of nitrate and decreased on King David by the use of potash. There was no potash experiment on Yellow Newtown.

The results on Winesap apples (reported in Tables IV, VIII, and X) were not so consistent. In 1921 water-core was decidedly less on this variety when nitrate was used, but in 1919 and 1922 there was slightly more of it. In 1921 the disease was less in amount when potash was used, but in 1922 there was more of it.

The results of the experiments as a whole indicate that applications of nitrate or potash fertilizer tend to prevent the development of water-core. The results are not sufficiently striking to recommend fertilizers as a remedy for the disease, but they certainly make it conclusive that the forcing of the fruit with potash or nitrate is not to be feared as an agency in the production of water-core. The reason for the favorable effects of fertilizers is considered later in connection with the studies on shade and maturity (pp. 21 and 24).

SIZE AND GROWTH RATE OF APPLES AS RELATED TO IRRIGATION, FERTILIZERS, AND WATER-CORE

In connection with the irrigation and fertilizer experiments, a study was made of the effect of the various treatments upon the size and the growth rate of the apples and also of the relation of size to the occurrence of water-core.

The effect of the various orchard treatments upon the size of the apples at picking time is shown on page 240, and in Tables III, VI, IX, and XIII. It would be expected that the plots receiving heavy irrigation and heavy applications of nitrate would show a relatively high percentage of large apples, but the data show that in general they had but little if any greater relative yield of the larger sizes than the unfertilized and lightly irrigated plots. The total yields from the heavily irrigated and nitrated plots averaged slightly higher than the yields from the others, and it is possible that this may account for their failure to distinctly surpass the others in percentage of large-sized apples.

Fortunately the question of growth stimulus was not left entirely to records on the picked fruit. Actual growth records were kept on apples from the different plots by repeated caliper measurements and by means of auxographs (MacDougal type) (*20*).

In the caliper work representative apples were tagged and their diameters measured at a particular hour of the day. A few days later another set of measurements was taken of the same apples at approximately the same hour. At the first reading the contact surfaces of the calipers were coated with blue wax, and this left a permanent mark on the apples that made it possible to take later measurements at the same point and along the same diameter. The jaws of the calipers had a spring release, thus applying the same pressure on the apples in the different readings.

The growth records for the apples in the irrigation plots of 1920 are shown in Figure 8. Equally striking contrasts were obtained in 1922, 1923, and 1924. In all cases the apples of the heavily irrigated plots enlarged very much more rapidly than those of the lightly irrigated ones.

The only complete growth record on the fertilizer plots was made in 1921, on the Jonathan variety. The record was based on caliper measurements of 25 representative apples from each plot. The apples of the nitrate plot increased from an average diameter of 1.865 inches on July 16 to an average diameter of 3.081 inches on

October 15; the apples of the potash plot from an average diameter of 1.873 inches to an average diameter of 2.967 inches in the same period, and the apples from the unfertilized plot from an average diameter of 1.823 inches to an average diameter of 2.919 inches. The average increase in diameter in the nitrate plot was 1.216 inches, in the potash plot 1.094 inches, and in the unfertilized plot 1.096 inches. This falls far short of the contrast obtained in the irrigation plots, but indicates that the growth rate of the apples in the nitrate plot was somewhat more rapid than that of the apples in the unfertilized plot.

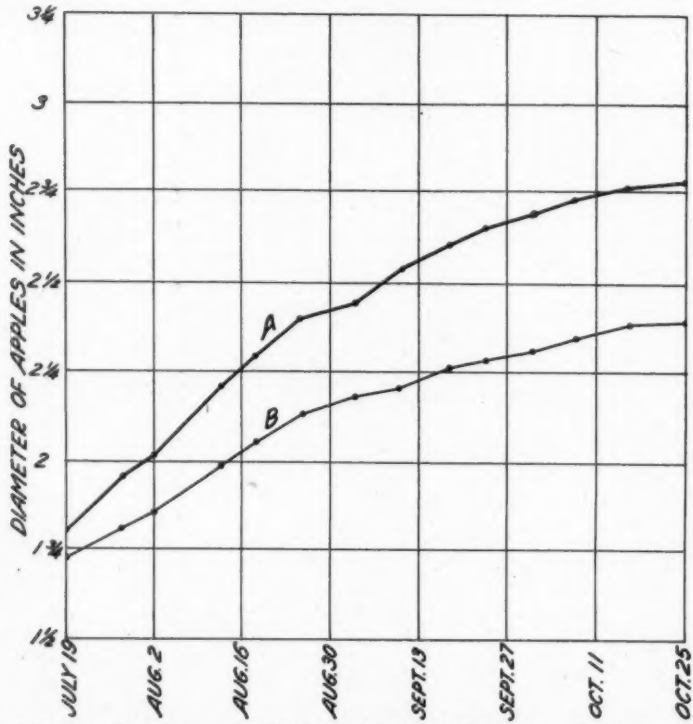

FIG. 8.—Growth rate of Winesap apples in the irrigation plots of 1920, based on caliper measurements of 25 different apples. (A) Heavily irrigated plot. (B) Lightly irrigated plot

In several preceding tables the percentage of water-core has been reported for the various sizes of apples as well as in totals for the different plots. In most cases the larger sizes had higher percentages of the disease than the smaller ones. The data of Tables IV, VII, and X, on the relation of size to water-core, are summarized in Figure 9 on the basis of the total apples of the different sizes. About 60 per cent of the 2¾ to 3 inch, the 3 to 3¼ inch, and the 3¼ to 3½ inch sizes have been affected with water-core, while only about 44 per cent of the apples that were 2¾ inches or less have been similarly affected. The disease is evidently more prevalent on the larger sizes.

The fact that the larger sizes of apples are more susceptible to water-core than the smaller ones would lead one to expect that orchard treatments which tended to increase the size of the fruit would be favorable to the development of the disease, but the results of the previous experiments do not support this hypothesis. Both heavy irrigation and heavy application of nitrate have been marked by increased growth rate of the apples, and both treatments have been accompanied by decrease rather than increase in the percentage of water-core. While water-core is somewhat more common on the large apples from a particular tree than on the smaller ones, as shown in Figure 9, it apparently does not follow that forcing apples into more rapid growth by irrigation or fertilizers will result in a higher percentage of the disease. The more vigorous foliage and the somewhat heavier crops on the fertilized and heavily irrigated trees may be of significance in explaining this seeming contradiction.

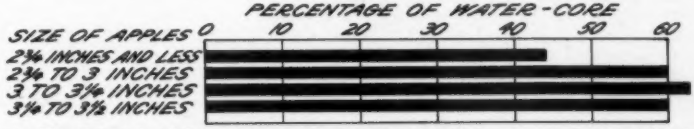

FIG. 9.—The effect of size of the apples upon the occurrence of water-core. A summary of Tables IV, VII, and X

EFFECT OF SHADE, SUNLIGHT, AND POSITION ON TREE UPON OCCURRENCE OF WATER-CORE

It was pointed out in the historical sketch at the beginning of this paper that it had been observed that water-core was not evenly distributed over the tree, but occurred most abundantly on the freely exposed fruit on the south or southwest side. In a number of the experiments of the present investigation a separate record was made for the apples from the different parts of the tree. The results are shown in Table XVI. The data are based on the total record of apples in the corresponding irrigation and fertilizer experiments previously reported. The apples described as exposed were from the more exposed limbs but were in partial shade. The apples described as shaded were from the more protected limbs, but received sufficient sunlight to have a high percentage of well-colored fruit.

A study of Table XVI shows that water-core was far more serious on the exposed than on the more or less shaded fruit. In the Winesap experiment of 1922, and in a very late picking of Jonathan in 1920, the exposed apples had but slightly more water-core than the shaded ones; but in three other experiments there was four times as high a percentage of the disease on the exposed apples as on the more protected ones; in two other cases twice as high a percentage; and in two instances the shaded apples were entirely free from water-core, with the exposed ones carrying a considerable percentage of the disease.

In some of the studies on the relation of the location in the tree to the occurrence of water-core, a record was made of the rate of evaporation under the different degrees of exposure. The results are shown in Table XVII. The atmometers in the tops of the trees were in partial shade, but were more exposed than those among the lower limbs. The different atmometers were intended to have the same relative exposure as the apples in the respective locations.

The results would indicate a considerably higher rate of evaporation in the more exposed locations. This may be of further interest when considered in connection with the studies on sap concentration on page 247.

TABLE XVI.—*Relation of the location on the tree to the susceptibility of apples to water-core*

Variety and date of picking	Percentage of water-core on apples from—			
	Exposed north	Shaded lower southwest	Exposed lower southwest	Exposed top
Northern Spy, picked Oct. 11, 1920		3.6	0	20.1
Winesap (fertilizer experiment) picked Oct. 13, 1920			23.5	23.0
Winesap (irrigation experiment) picked Oct. 25, 1920		33.3	63.9	79.7
Jonathan, picked Sept. 22, 1921		2.3		7.4
Jonathan, picked Oct. 15, 1921		60.4		65.2
Jonathan, picked Sept. 22, 1922	16.1	15.8	52.7	69.1
Winesap, picked Oct. 24, 1922	85.9	60.6	86.3	90.9
Winesap, picked Oct. 21, 1923		49.9		88.1
Rome Beauty, picked Oct. 4, 1924	0	0	17.7	

	Shaded interior	Exposed top and lower southwest
Jonathan, picked Sept. 6, 1924	0	5.5
King David, picked Sept. 5, 1924	0	0.6
Rome Beauty, picked Oct. 4, 1924	3.1	32.5

TABLE XVII.—*Rate of evaporation at different locations in the same tree*

Variety, treatment, and period of observation	Evaporation ratio (cubic centimeters evaporated per atmometer).	
	In top partially shaded	In shade of lower limbs
Yellow Newtown, Aug. 23 to 30, 1919:		
Heavily irrigated	172.5	148.5
Lightly irrigated	188.0	157.0
Winesap, July 19 to Sept. 18, 1920:		
Heavily irrigated	184.6	174.4
Lightly irrigated	200.0	192.1
Jonathan, July 1 to Sept. 22, 1922	1,860.3	1,341.0

In the 1923 Jonathan experiments on fertilizers, the apples were sorted at picking time into different lots on the basis of color and sunburn, and separate records were made as to the percentage of water-core. In a picking made September 14, the bright-red apples with a touch of sunburn had 31 per cent of water-core, and the bright-red apples with no sunburn 3 per cent. In a picking made October 5, the apples showing more or less sunburn had 57 per cent of water-core, and the bright-red apples without sunburn had 46 per cent.

The contrasts shown in Table XVI and in the Jonathan apples that were graded on the basis of color and sunburn are very significant as to the relation of sunlight to water-core, but they fall far short of the contrasts obtained from examination of individual apples

and groups of apples as picked from the tree. It was often found that water-core was confined entirely to a few scattering apples that were extremely exposed and had developed a slight sunburn. In many cases it was possible to go over the trees and pick out the water-core apples by their location on the tree and their high but bronze-tinted color. It was also observed that the apples from trees that were devitalized and carried a sparse foliage were likely to be affected with water-core.

It was quite common with sunburned apples for the more exposed half to be affected with water-core and the shaded half to be entirely free from the disease.

A number of experiments were made to determine the effect of artificial shade or inclosure upon the development of water-core. Apples or clusters of apples were selected before water-core had begun to appear, and some of these were covered with glassine bags or medium-grade muslin sheeting, and the others were left freely exposed. The glassine bags were translucent and reduced the amount of light reaching the apples. They were practically impervious to water, and were tied so as to enclose the individual apples, thus tending to restrict transpiration. The muslin was pinned over clusters of apples without actually inclosing them. It reduced the light and lowered the temperature, but without any great restriction in the air movement over the apples. The effect of these treatments upon water-core is shown in Table XVIII.

TABLE XVIII.—*Effect of artificial shade or inclosure upon the development of water-core*

Variety	Date when shaded	Date of picking	Percentage of water-core in—		
			Apples in glassine bags	Apples shaded by muslin	Apples not shaded
Yellow Transparent	July 2, 1921	July 25, 1921	28.0	.....	20.2
Jonathan	Aug. 13, 1921	Oct. 15, 1921	78.3	.....	66.7
Winter Banana	Aug. 6, 1923	Aug. 24, 1923	24.6	.....	16.1
Do	....do....	....do....	.....	5.3	32.7
Do	July 30, 1924	Aug. 22, 1924	.....	0	69.0
Jonathan	Aug. 31, 1923	Sept. 14, 1923	.....	0	21.7
Do	....do....	Oct. 5, 1923	.....	53.5	47.6
Winesap	Sept. 4, 1923	Oct. 31, 1923	.....	64.4	75.9
King David	July 30, 1924	Sept. 6, 1924	.....	0	2.4
Do	....do....	Sept. 25, 1924	.....	65.0	78.6

The glassine bags apparently favored the development of water-core, but the muslin shading apparently decreased the disease, and the decrease was very decided except in instances of very late picking, where even the apples in the shade developed a high percentage of water-core.

A study of the data from various experimenters shows that the degree of shade and the intensity of the sunlight had a greater bearing on the occurrence of water-core than irrigation or fertilizers. In view of this fact it seems probable that at least a part of the favorable effect of fertilizers and heavy irrigation should be attributed to a greater shading resulting from heavier foliage.

No studies have been completed as to the relative importance of the light and heat effects of sunlight in the production of water-core,

but the writers are of the opinion that temperature is more significant than light. Air temperatures of 90° to 100° F. are not uncommon in Wenatchee, and, as was pointed out in an earlier publication,[3] the exposed side of exposed apples may often have a temperature 15° to 20° F. higher than that of the air in the shade.

EFFECT OF MATURITY OF THE FRUIT UPON THE DEVELOPMENT OF WATER-CORE

In some of the experiments, several different pickings were made and the percentage of water-core was determined for each picking. The apples were taken as they came on the tree without any selection as to color or ripeness. The early pickings were made at the very beginning of the commercial harvesting period for the variety, and the late pickings after the usual harvesting period had passed. The results are shown in Table XIX.

TABLE XIX.—*The relation of the date of picking to the prevalence of water-core*

Variety and year	Picked early		Picked late	
	Date	Percentage of water-core	Date	Percentage of water-core
Jonathan, 1921	Sept. 22	4.9	Oct. 14	68.8
Jonathan, 1923	Sept. 14	13.6	Oct. 5 Nov. 4	50.0 97.9
Jonathan, 1924	Sept. 6	1.4	Sept. 27	96.5
King David, 1924	Sept. 5	0.6	Sept. 25	78.5
Winesap, 1924	Oct. 3	2.6	Oct. 27	95.6

In the early pickings there was about 14 per cent of the disease in one instance, but less than 5 per cent in all other cases, while in the late pickings 50 to 98 per cent of the apples were affected. During and immediately following the harvesting season there was an enormous increase in the disease.

In 1924 the maturity of the early and late picked Jonathan apples was determined by pressure tests. On September 6 the fruit tested 16 pounds, while on September 27 it tested 14.5 pounds. With a softening represented by 1.5 pounds difference in resistance to pressure, the water-core increased from 1.4 per cent to 96.5 per cent (Table XIX). Nearly all of this increase in the disease occurred during the latter half of the period covered, since an additional picking made on September 16 was found to be practically free from water-core.

If the results of Table XIX are compared with those reported in the previous pages, it becomes evident that the question of the maturity of the fruit completely overshadows the effects of irrigation and fertilizer and stands with exposure to sunlight as one of the prime determining factors in the occurrence of water-core. It would seem from the data collected that if rains during the harvesting season appear to result in an increase in water-core, as various writers have reported, careful consideration should be given to the possibility of the apples having become overmature as a result of the delays occasioned by the rain or because of undue waiting for color.

[3] BROOKS, C., and FISHER, D. F. SOME HIGH TEMPERATURE EFFECTS IN APPLES: CONTRASTS IN THE TWO SIDES OF AN APPLE. Jour. Agr. Research 32: 1-16, illus.

It is evident in the data reported on pages 22 and 23, and it was noted in other cases, that in the earlier pickings water-core was confined largely to the more exposed fruit, but that in the late pickings it was often found on the shaded as well as the sunburned apples. This fact should be of further interest in connection with the studies on sap concentration.

SAP CONCENTRATION AND ACIDITY IN RELATION TO WATER-CORE

The fact that water-core decreased with heavy irrigation and with application of fertilizer, and increased with intensity of sunlight and with overmaturity, made it seem probable that studies on sap concentration and acidity might throw some light on the nature of the disease. Tests along this line were started in the summer of 1923.

A study was made of both leaf and fruit tissues. The material was collected from various representative locations on the limb or tree and placed immediately in tight containers. The osmotic determinations on the leaves were made upon return to the laboratory, and those on the apples usually within a few hours after collection. Ten to twenty apples were included in each sample. Usually the whole apple was not ground, but a part of each apple included in a composite sample. The samples to be compared were taken from the same relative position on the apple with reference to the blush area and consisted of wedge-shaped longitudinal sections extending to the core.

The leaf and apple tissue was ground in a small meat chopper and the juice was extracted by means of a tincture press The osmotic determinations were made by the freezing-point method with a Beckmann thermometer. The results of the various tests are given in Tables XX, XXI, XXII, XXIII, XXIV, and XXV.

Extractions with and without freezing the tissue gave practically no contrast in sap concentration; and as a part of the juice was to be used later in sugar analyses the authors considered it advisable to make the extractions by the latter method. All of the data reported were obtained from extractions made without freezing the tissue.

The data reported on Winesap in Table XX show that the sap concentration of both the foliage and fruit was greater in the afternoon than in the morning. This fact is in agreement with the experimental results on other plants reported by various writers.

It will be seen from Tables XX and XXI that the sap concentration was greater in the leaves than in the apples, showing, as has been pointed out by Chandler (*10*) and others, that the foliage is able to draw water away from the fruit in cases where the supply is insufficient for both.

The sap concentration and acidity tests from the irrigation plots are shown in Table XX. In 5 tests on Winesap leaves, 6 on Winesap apples, and 2 on King David leaves the sap concentration was decidedly greater in the lightly irrigated plot than in the heavily irrigated one, while in 3 tests on King David apples the lightly irrigated plot showed a lower sap concentration than the heavily irrigated one. In general, the results probably can be said to indicate that an increase in irrigation tends to produce a decrease in sap concentration. It should be recalled in this connection that the

apples from the heavily irrigated plots had a slightly lower percentage of water-core than those from the lightly irrigated plots (Tables XII and XIV).

TABLE XX.—*Effect of irrigation upon sap concentration and acidity (collections at different times in the day)*

Description of samples	Osmotic pressure in atmospheres		Acidity in cubic centimeters of N/10 NaOH required to neutralize 10 cubic centimeters of extract	
	Heavy irrigation	Light irrigation	Heavy irrigation	Light irrigation
Winesap, 1923:				
Leaves collected—				
10 a. m. Aug. 15	20.63	23.94		
5.30 a. m. Aug. 30	18.82	20.45		
2.30 p. m. Aug. 30	22.86	23.64		
9 a. m. Sept. 11	20.93	20.93		
3 p. m. Sept. 11	25.86	26.47		
Apples collected—				
10 a. m. Aug. 15	12.45	13.65	13.8	13.5
5.30 a. m. Aug. 30	13.41	14.44	10.3	11.0
2.30 p. m. Aug. 30	14.56	15.04	10.7	10.4
9 a. m. Sept. 11	14.80	15.04	10.0	9.3
3 p. m. Sept. 11	15.76	15.70	9.3	10.7
Apples picked Oct. 22, samples taken Nov. 1	17.92	18.11	7.6	7.4
King David, 1924:				
Leaves collected 9.30 a. m. July 19, 18 hours after the completion of a 3-day irrigation on both plots	23.44	24.82		
Leaves collected 10 a. m. July 28	27.39	27.87		
Apples collected 9.30 a. m. July 19, 18 hours after the completion of a 3-day irrigation on both plots	15.88	15.76	9.9	10.0
Apples collected 10 a. m. July 28	16.48	16.30	10.35	10.75
Apples picked Sept. 5 and stored at 70° F. till Sept. 9	23.56	21.76	7.35	6.05

TABLE XXI.—*Effect of nitrate and potash fertilizers upon sap concentration and acidity*

Description of samples	Osmotic pressure in atmospheres			Acidity in cubic centimeters of N/10 NaOH required to neutralize 10 cubic centimeters of extract		
	Potash	Nitrate	Untreated	Potash	Nitrate	Untreated
Jonathan, 1923:						
Collected Sept. 14—						
Red apples, not sunburned	20.33	22.86	21.29	9.5	9.3	8.5
Red apples, slightly sunburned	23.70	26.59	24.18	8.5	7.2	7.9
Collected Sept. 22—						
Red apples, not sunburned		22.44	20.57		8.6	9.2
Red apples, slightly sunburned		23.52	21.53		8.2	7.4
Collected Oct. 6—						
Red apples, not sunburned	20.27	19.85	20.43	9.8	9.0	9.2
Red apples, slightly sunburned	22.01	23.58	23.70	8.5	9.1	7.8
Jonathan, 1924:						
Collected 10 a. m. July 21—						
Leaves, fertilizer in 1924 only	22.96	26.13	26.07			
Leaves, fertilizer for 4 years	26.01	24.40				
Apples, fertilizer in 1924 only	14.80	16.06	15.10	9.85	10.0	9.5
Apples, fertilizer for 4 years	15.40	15.46		9.8	9.2	
King David, 1924:						
Leaves collected 9.30 a. m. July 19		24.16	23.44			
Leaves collected 10 a. m. July 28		27.87	27.39			
Apples collected 9.30 a. m. July 19		15.69	15.88			
Apples collected 10 a. m. July 28		16.36	16.48		11.6	10.35
Apples picked Sept. 5, determinations Sept. 9		23.56	23.56		7.35	7.95

The results of sap concentration and acidity tests from the fertilizer plots are given in Table XXI. The data are not always consistent, but in most cases the sap concentration of the apples from the nitrate plots was higher, and that from the potash plots somewhat lower, than that of the apples from the unfertilized plots. In Table XV it was shown that at the time of commercial picking the apples from the Jonathan nitrate and potash plots of 1923 and 1924 had slightly less water-core than the apples from the untreated plots.

TABLE XXII.—*Relation of shade and location on the tree to sap concentration and acidity*

Description of samples	Osmotic pressure in atmospheres		Acidity in cubic centimeters of N/10 NaOH required to neutralize 10 cubic centimeters of extract	
	Exposed	Shaded	Exposed	Shaded
Natural shade:				
Winter Banana, collected Aug. 23, 1923—				
Leaves from lower limbs	27.55	22.62		
Apples from lower limbs	15.40	14.20	13.2	11.6
Apples from the top of the tree	16.36		12.4	
Winesap apples, collected Nov. 3, 1923—				
From lightly irrigated plot *	17.08	16.60	8.6	7.6
From heavily irrigated plot *	16.90	15.76	7.6	
Light irrigation followed by heavy *	19.25	16.96	7.6	8.3
As above, but apples with poor color		16.54		7.8
Winter Banana apples, collected Aug. 5, 1924—				
Good color	16.30	15.64	6.7	6.8
Poor color	16.00	15.16	7.0	6.9
Artificial shade with muslin:				
Winter Banana, shade applied Aug. 6, collected Aug. 24, 1923—				
Apples slightly sunburned	17.08	16.60	8.4	7.6
Apples not sunburned	16.12	14.98	9.7	8.3
Jonathan, shade applied Aug. 3—				
Collected Oct. 5, 1923—				
Apples with high color	23.70	19.91	7.8	8.3
Apples with poor to medium color	20.43	19.25	9.2	8.8
Collected Nov. 5, overripe	20.21	20.45	8.9	7.9
Winesap, shade applied Sept. 4, 1923, collected Oct. 31—				
Light irrigation, apples with good color	18.11	17.44	7.4	7.3
Light irrigation, apples with poor color		17.38		6.5
Heavy irrigation, apples with good color	17.92	17.14	7.6	7.6
Heavy irrigation, apples with poor color		17.41		7.6
Winter Banana, shade applied July 25, 1924, apples collected Sept. 11	16.24	14.44	3.6	3.9

* Shaded fruit well colored; exposed fruit deep red color.

The effects of exposure and of natural and artificial shade are shown in Table XXII. The apples which were well exposed to sunlight had a decidedly higher sap concentration than those which received various degrees of shading. This was true with both the highly colored and the poorly colored fruit. In Table XVII it was pointed out that the rate of evaporation was greater in the exposed locations in the tree than in the more shaded ones, and in Tables XVI and XVIII it was shown that the apples from the more exposed locations were much more susceptible to water-core than those that received a considerable degree of natural or artificial shade.

TABLE XXIII.—*Relation of sunburn to sap concentration and acidity; contrasts between the opposite sides of the same apples*

Description of material	Osmotic pressure in atmospheres		Acidity in cubic centimeters of N/10 NaOH required to neutralize 10 cubic centimeters of extract	
	Sunburned	Not sunburned	Sunburned	Not sunburned
Comparing sunburned apples with highly colored ones that were not sunburned:				
Winter banana—				
Collected Aug. 23, 1923	17.50	16.36	11.6	12.4
Collected Aug. 24, 1923	17.08	16.12	8.4	9.7
Collected July 22, 1924	19.18	16.87	7.4	7.6
Collected Aug. 8, 1924	19.12	17.32	4.2	5.5
Jonathan, 1923:				
From nitrate plots, Sept. 14	26.59	22.86	7.2	9.3
From potash plots, Sept. 14	23.70	20.33	8.5	9.5
From unfertilized plots, Sept. 14	24.18	21.29	7.9	8.5
From nitrate plots Sept. 22	23.52	22.44	8.2	8.6
From unfertilized plots, Sept. 22	21.53	20.57	7.4	9.2
From nitrate plots, Oct. 6	23.58	19.85	9.1	9.0
From potash plots, Oct. 6	22.01	20.27	8.5	9.8
From unfertilized plots, Oct. 6	23.70	20.43	7.8	9.2
Rome Beauty—				
Collected Oct. 2, 1923	18.17	16.84	3.5	5.2
Comparing the sunburned quarters of apples with the opposite quarters:				
Winter Banana, July 22, 1924	19.60	18.76	7.1	7.8
Do	15.88	13.96	5.9	6.3
Winter Banana, Aug. 5, 1924	19.12	17.08	5.7	----------

TABLE XXIV.—*Relation of sap concentration and acidity to water-core*

Description of material	Osmotic pressure in atmospheres		Acidity in cubic centimeters of N/10 NaOH required to neutralize 10 centimeters of extract	
	Water-core	No water-core	Water-core	No water-core
Water-core apples and similar apples free from water-core:				
Winter Banana—				
Aug. 5, 1924	19.12	16.30	5.7	6.7
Aug. 14, 1924	18.70	16.24	5.3	6.0
Aug. 16, 1924	18.46	15.47	4.9	5.3
Aug. 19, 1924	19.00	14.56	3.3	5.2
Aug. 21, 1924	19.24	17.08	4.8	5.2
Do	18.28	15.58	5.6	5.7
Sept. 11, 1924	17.68	15.04	3.1	4.0
Sept. 23, 1924	16.84	15.64	3.1	3.1
Winesap, Sept. 23, 1924	18.58	17.20	3.8	5.1
Water-core tissue and normal or only slightly water-cored tissue from the same apples:				
Winter Banana, Aug. 25, 1923	19.85	15.64	6.0	10.4
Rome Beauty, Oct. 2, 1923	18.65	17.68	3.7	3.2
Winter Banana, Aug. 21, 1924	19.24	19.00	4.8	4.8
Winesap, Sept. 23, 1924	19.72	17.44	3.4	4.3
Opposite quarters of the same apples (cut longitudinally to the core):				
Winter Banana—				
Aug. 5, 1924	19.84	17.08	4.9	5.7
Aug. 8, 1924	19.12	17.32	4.2	5.6
Aug. 14, 1924[a]	19.36	18.04	4.8	5.8
Aug. 16, 1924[b]	19.84	17.08	3.6	5.2
Aug. 19, 1924[a]	19.00	15.64	3.3	4.6
Aug. 21, 1924[a]	18.88	17.68	5.3	5.8
Sept. 11, 1924[a]	19.12	16.24	2.7	3.6

[a] Bad water-core. [b] Flecked with water-core.

The contrasts between sunburned fruit and well-colored fruit that was not sunburned are shown in Table XXIII. The sunburned fruit had a much higher sap concentration in all of the tests, and it usually had a lower acidity, than the fruit that was free from sunburn. The sunburned quarters of exposed apples also had a higher sap concentration and lower acidity than the opposite quarters. It was pointed out on page 245 that sunburned apples were particularly susceptible to water-core.

The sap concentration and acidity of water-core apples is shown in Table XXIV. It will be seen that the water-core tissue had a higher sap concentration and lower acidity than the normal tissue. This was true whether the water-core apples were compared with normal apples, the water-core tissue with sound tissues of the same apples, or the quarters of the apples affected with water-core with the opposite quarters that were free from the disease. The contrasts were striking in practically all cases, the sap concentration of the water-core tissue running two to four atmospheres higher than that of the normal tissue and the average acidity of the normal tissue some 14 per cent higher than that of the water-core tissue. It was pointed out in an earlier publication[4] that the sap concentration on the blush side of an apple is often three-fourths of an atmosphere higher than that on the opposite side of the same apple. In a number of the instances reported in Table XXIV, where the quarters of apples affected with water-core were compared with the opposite quarters, a similar comparison was made at the same time with the blushed and shaded quarters of normal apples. The sap concentration of the normal tissue of the water-cored apples ran a half to one and a half atmospheres higher than the sap concentration of the blush side of normal apples, and one to three atmospheres higher than the sap concentration of the greener or shaded side of the normal apples. Evidently high sap concentration is characteristic not only of water-core tissue but also, in lesser degree, of the sound tissue of water-core apples.

The collections of Tables XX to XXIV, inclusive, were made at different times and from various orchards, and most of them do not, therefore, give an opportunity for a study of the seasonal trend of sap concentration. Repeated collections, however, were made from some of the orchards and under conditions that would allow a seasonal comparison. The results are shown in Table XXV. There was usually a gradual increase in sap concentration, and a decrease in acidity, during and preceding the normal picking season. The Jonathan data seem to be an exception to this rule, but in this case the collections were all made after the normal picking season.

A comparison of the results on sap concentration with those on water-core shows a close agreement throughout, unless an exception be made in regard to the nitrate fertilizers. Neither sap concentration nor water-core was greatly affected by fertilizers or irrigation, but in the potash and irrigation experiments the conditions which resulted in a lower sap concentration also resulted in a decrease in water-core, while in the nitrate experiments this was apparently not true. It is possible that the better foliage, the increased shade, and

[4] BROOKS, C., and FISHER, D. F. SOME HIGH TEMPERATURE EFFECTS IN APPLES: CONTRASTS IN THE TWO SIDES OF AN APPLE. Jour. Agr. Research 32: 1-16, illus. 1926.

the later maturing of the apples in the nitrate plot more than offset the effect of the higher sap concentration as far as water-core was concerned.

TABLE XXV.—*Relation of time of picking to sap concentration and acidity*

	Osmotic pressure in atmospheres		Acidity in cubic centimeters of N/10 NaOH required to neutralize 10 cubic centimeters of extract	
	Normal apples	Sound tissue from sunburned or water-core apples	Normal apples	Normal tissue from sunburned or water-core apples
Jonathan, 1923:				
Collected Sept. 14	21.29	24.18	8.5	7.9
Collected Sept. 22	20.57	21.53	9.2	7.4
Collected Oct. 6	20.43	23.70	9.2	7.8
King David, 1924:				
Collected July 19	15.77	----------	9.9	----------
Collected July 28	16.39	----------	10.45	----------
Collected Sept. 5	22.96	----------	7.1	----------
Winter Banana, 1924:				
First orchard—				
Collected July 22, 1924	14.50	13.96	6.3	6.3
Collected Aug. 19	14.32	15.64	5.1	4.6
Collected Sept. 23	17.20	17.44	5.1	4.3
Second orchard—				
Collected Aug. 5, 1924	15.40	17.08	6.9	5.7
Collected Aug. 21	16.60	19.01	5.4	4.8
Winesap, 1923:				
Heavy irrigation—				
Collected Aug. 15	12.45	----------	13.8	----------
Collected Aug. 30	14.56	----------	10.7	----------
Collected Sept. 11	15.76	----------	9.3	----------
Collected Oct. 22	17.92	----------	7.6	----------
Light irrigation:				
Collected Aug. 15	13.65	----------	13.5	----------
Collected Aug. 30	15.04	----------	10.4	----------
Collected Sept. 11	15.70	----------	10.7	----------
Collected Oct. 22	18.11	----------	7.4	----------

In all of the other experiments the correlation was very striking. Exposed apples and sunburned apples had a much higher sap concentration than the more protected ones, and were far more susceptible to water-core; and the exposed and sunburned sides or quarters of apples had a much higher sap concentration and a far greater susceptibility to water-core than the opposite sides or quarters. Apples increased in sap concentration with maturity with a parallel increase in susceptibility to water-core. The results show that a high-sap concentration is an accompaniment of water-core, and they suggest that it has a close connection with the cause of the disease.

The fact that sap concentration and susceptibility to water-core both increase with maturity would give further emphasis to the importance of picking the apples at the proper time. It should be noted, however, that water-core apples collected early in the season had a higher sap concentration than normal apples collected late in the season and it should be kept in mind that the sap concentrations that accompany water-core represent a diseased condition and one not to be found in normal apples.

PARTIAL RECOVERY IN STORAGE

The grower who finds his harvested fruit affected with water-core still has hopes of recovery in storage. To just what extent water-core apples can be expected to recover in storage is an important question in determining the disposition of the fruit. In a number of the experiments previously reported some of the affected apples were followed through storage to obtain evidence on this point. In most cases water-core was not evident in surface view so it was necessary to cut open some of the apples at each inspection. Water-core apples have a higher specific gravity than those which are not water-cored, but it was not found possible to use this characteristic as a means of detecting mild cases of the disease. It was found, however, that the water-core tissue gave a better transmission of light than the normal tissue, and could be fairly well located by a candling process similar to that used on eggs. A 100-watt electric lamp was used as the source of light. The "candling" method was of considerable value in determining the nature and extent of the disease, but it was always checked by data obtained by the actual cutting of the apples.

In the 1919 experiments, notes were taken on part of the Winesap and Yellow Newtown apples on November 12, and similar lots were held in cellar storage till March 9 and 10 for later notes. The cellar temperature ranged from 0 to 8° C. (32° to 46.4° F.) and averaged about 4° C. (39.2° F.). In the November notes 15 bushels of Winesap and 25 bushels of Yellow Newtown were included in the record, and in the March notes 5 bushels of Winesap and 12 bushels of Yellow Newtown. The results are shown in Table XXVI.

TABLE XXVI.—*Behavior of water-core apples in cellar storage, 1919 experiments*

Size of apples	Percentage of apples affected				
	Winesap		Yellow Newtown		
	Water-core Nov. 12, 1919	Water-core Mar. 10, 1920	Water-core Nov. 12, 1919	Water-core Mar. 10, 1920	Internal browning Mar. 10, 1920
2¾ inches and less	45.5	1.6	8.2	0.5	27.4
2¾ to 3 inches	69.2	3.0	21.5	0.0	46.8
3 to 3¼ inches	72.3	13.9	33.3	2.4	62.4
3¼ to 3½ inches	69.0	44.4	49.8	1.7	79.7

During the four months of storage, water-core disappeared almost entirely from the Yellow Newtown and from the two smaller sizes of Winesap. With the 3 to 3¼ inch Winesap it was reduced to about one-fifth the former amount, and with the 3¼ to 3½ inch size to about two-thirds the percentage found on the earlier date.

At the time of the March record a few of the Winesap had a brownish tint in the region of the large vasculars that was apparently an after effect of water-core, but in most cases the apples that were free from water-core appeared entirely normal. With the Yellow Newtown a very different condition prevailed; water-core had disappeared but internal browning[5] had developed. In the examination of

[5] The typical internal browning of Yellow Newtown, characterized by a browning of the flesh without distinct softening.

November 12 only 0.4 per cent of the apples showed internal browning, while it will be seen from Table XXVI that in the examination of March 10, 27 to 80 per cent of the apples were affected. There was a much higher percentage of this trouble in March than there was of water-core in November, indicating that much of the browning did not actually follow water-core, but there was a close correlation between the two diseases in the susceptibility of the different sizes of apples and in the location and pattern of the affected tissues, and the water-core tissue that remained frequently had a margin of typical browning (pl. 1, D). These facts, together with the almost complete disappearance of the watery tissue during storage, would indicate that a considerable part of the internal browning was an after-effect of water-core.

In the November examination of Yellow Newtown, 15 apples were found with water-core that was visible on the surface, and these were held in storage as a separate lot. In the March examination 1 apple had entirely recovered, 3 had internal browning and no water-core, 6 had internal browning with some water-core, and 5 remained apparently unchanged. From the commercial standpoint, it might be said that there was practically no recovery in storage with this lot.

In 1920 storage tests were made on Winesap and Stayman Winesap that were affected with water-core. The apples were mostly of the smaller sizes. There was 1 box of Stayman Winesap and 2 to 4 boxes of Winesap under each storage condition. The Stayman Winesaps were in storage from November 5 till March 20, and the Winesaps from November 6 till June 18. The results are shown in Table XXVII.

TABLE XXVII.—*Behavior of water-core apples in storage, 1920 experiments*

	Percentage of apples affected					
	Before storage			After storage		
	With water-core	With browned vasculars	With internal breakdown	With water-core	With browned vasculars	With internal breakdown
Stayman Winesap:						
In cellar storage	Very high.			42		45
In cold storage	Very high.			41		47
Winesap, first orchard:						
In cellar storage	73.1	0	0	0	0	63.2
Winesap, second orchard:						
In cellar storage	93.0	2	0	0	28.2	0
In cold storage	93.0	2	0	0	36.7	2.7

The Stayman Winesap made little recovery, either in cellar or commercial cold storage, such disappearance of water-core as occurred being offset by the development of internal breakdown.[6] The Winesap made a complete recovery in both cellar and cold storage so far as water-core itself was concerned, but a very high percentage of the apples developed either internal breakdown or browned vascular tissue. The final notes were taken June 18, which is late in the season but no later than Winesap are often held.

[6] A browning and softening of the flesh, particularly common in overmature fruit.

In 1921, four boxes of badly water-cored Winter Banana apples were held in storage. Nearly all of the apples had visible water-core when they went into storage, and the weight and appearance of the others indicated that they were also affected with the disease. Two boxes of the apples were held in an air-cooled basement storage and the other two in commercial cold storage; the apples in the cellar storage were of the 72 and 80 sizes (number of apples to the box), while those in cold storage were of the 100 and 113 sizes. It was found on January 25 that none of the apples from cellar storage had water-core, and only 1.9 per cent of those from cold storage were affected, but 88 per cent of the cellar-storage apples and 85 per cent of the cold-storage ones had developed internal breakdown, a large part of which appeared to be centered in the tissue that had originally been affected with water-core.

In 1922, water-core notes were taken on November 4 on some of the apples from the Winesap irrigation and fertilizer plots (see p. 235), and the rest of the crop (approximately three boxes from each orchard condition) was held in cellar storage till January 18, when notes were taken again. The results are shown in Table XXVIII. There was practically no visible water-core at the time of the first note-taking, and in most cases the affected tissue was confined to small areas between the carpel walls or around the main vasculars.

TABLE XXVIII.—*Behavior of water-core on Winesap apples in storage, 1922 experiments*

Plot and orchard treatment	Percentage of water-core on apples of the following sizes							
	2¾ inches or less		2¾ to 3 inches		3 to 3¼ inches		3¼ to 3½ inches	
	Nov. 4	Jan. 18	Nov. 4	Jan. 18	Nov. 4	Jan. 18	Nov. 4	Jan. 18
1. Heavy irrigation (records of Nov. 4 and Nov. 23 combined)	54.9	5.1	70.0	1.7	88.7	0	88.9	0
2. Light irrigation (records of Nov. 4 and Nov. 23 combined)	77.4	13.4	82.1	16.5	89.4	26.3	80.0	0
3. Light irrigation followed by heavy	38.3	24.1	57.1	41.0	86.7	56.4	100.0	66.7
4. Heavy irrigation followed by light	67.2	4.9	82.4	23.1	84.6	40.0		
5. Nitrate of soda	87.5	40.9	94.8	32.4	98.4	38.3	100.0	40.0
6. Muriate of potash	86.2	4.1	92.7	5.8	98.2	6.5	100.0	0
Total for all plots	63.0	8.8	77.8	19.4	92.7	32.0	94.6	24.0

The recovery from water-core in storage was not so complete as in the 1919 and 1920 experiments, but the notes were taken much earlier. The apples from the heavy irrigation and potash plots made the most complete recovery. It will be seen from the totals for all the plots that the smaller-sized apples made a much more complete recovery than the larger-sized ones. With the apples that were 2¾ inches or less water-core was reduced in storage to about one-seventh the original amount; with the 2¾ to 3 inch apples to about one-fourth the original amount; and with the 3 to 3¼ inch apples to about one-third the original amount. In a few instances water-core was followed by internal breakdown, but in most cases the previously water-cored apples had no evident after effects of the disease.

TABLE XXIX.—*Behavior of water-core apples in storage, 1923 experiment*

Variety and orchard treatment	Percentage of apples affected			
	Before storage		After storage	
	Water-core	Internal breakdown	Water-core	Internal breakdown
Jonathan; in cellar storage Oct. 5 to Feb. 2:				
From nitrate plot	34.6	0	0	0
From potash plot	71.8	0	0	6
From unfertilized plots	47.2	0	0	29.2
Mixed lot from all the plots:				
In oiled wraps	50.2	0	0	7.6
In common wraps			0	0
Winesap; in cellar storage Oct. 3 to Apr. 10:				
Heavy irrigation	57.5	0	0	0
Light irrigation	67.1	0	0	0
Heavy irrigation followed by light	82.5	0	1.2	0
Light irrigation followed by heavy	88.2	0	0	0
Rome Beauty, in cellar storage Oct. 10 to Apr. 10	100	0	7.3	89.1

Some of the apples from the 1923 orchard experiments were also held in storage for further notes on water-core. The results are shown in Table XXIX. While water-core was bad at picking time, the recovery in storage was practically complete on both Jonathan and Winesap. Some internal breakdown developed on Jonathan, apparently as an aftereffect of water-core, but the Winesap apples from the lots that had previously shown 57 to 88 per cent of water-core came out of storage practically free from the disease and apparently entirely normal. The water-core on both these varieties was invisible (not evident in surface view). The Rome Beauty apples, on the other hand, had a high percentage of visible water-core when they went into storage, and while it will be seen that most of the disease disappeared as such, a high percentage of internal breakdown developed apparently as an aftereffect of the water-core.

TABLE XXX.—*Water-core apples in cold storage and cellar storage (Winesap, 125 size, 1923)*

Condition of storage and date of note taking	Percentage of apples			
	Sound	With water-core		With internal breakdown
		Slight	Bad	
Before storage, Nov. 16	1.6	63.7	34.7	0
After cellar storage, Apr. 12:				
In oiled wrappers	48.5	33.6	10.0	7.9
In common wrappers	52.2	32.1	12.6	3.1
After cold storage, Apr. 16:				
In oiled wrappers	53.3	41.6	3.2	1.9
In common wrappers	34.8	32.6	23.9	8.7
After cellar storage, May 15:				
In oiled wrappers	54.6	41.9	1.2	2.3
In common wrappers	60.5	34.4	1.7	3.4
After cold storage, May 15:				
In oiled wrappers	40.0	54.1	1.2	4.7
In common wrapper	39.8	48.3	3.5	8.4

Badly water-cored Winesap apples from another orchard were used in a comparison of cellar storage and cold storage, and in tests on different kinds of wrappers. The results are shown in Table XXX. Practically all of the apples had water-core when they went into storage, and about half of them recovered from the disease. The recovery was slightly better in cellar storage than in cold storage, and practically the same in the oiled wrappers as in the common wrappers.

In 1924, storage experiments were carried out on badly water-cored Jonathan, Delicious, and Arkansas (Mammoth Black Twig). The results are shown in Table XXXI.

TABLE XXXI.—*Behavior of water-core apples in storage, 1924 experiments*

Variety and size of apples, and the conditions of storage	Percentage of apples affected			
	Before storage		After storage	
	Water-core	Internal breakdown	Water-core	Internal breakdown
Jonathan, in cellar storage about 70° F.:				
Sept. 17 to Sept. 26	8.8		1.1	
Sept. 29 to Oct. 18—				
2¾ inches or less	93.4	0	31.6	27.4
2¾ to 3-inch size	97.3	0	42.3	44.4
3 to 3¼-inch size	100	0	36.1	42.6
3¼ to 3½-inch size	100	0	75	100
Delicious:				
In air-cooled storage—				
Oct. 3 to Dec. 17	100	0	75	0
Oct. 3 to Mar. 30	100	0	0	43.5
In cold storage—				
Oct. 3 to Feb. 10	100	0	29.8	0
Oct. 3 to Apr. 25	100	0	35.8	26.9
Arkansas (Mammoth Black Twig), in cold storage, Oct. 14 to Mar. 30	100	0	0	0

The Jonathan were held in cellar storage, and while one-half to two-thirds of the water-core disappeared within 3 weeks, a considerable amount of internal breakdown developed in its place. The recovery was better on the apples 2¾ inches or less in size than it was on the larger sizes.

In air-cooled storage, 25 per cent of the Delicious recovered by December 17 and water-core had disappeared from all of them by March 30 but on the latter date 43.5 per cent of the formerly water-cored apples had developed internal breakdown. In cold storage, about two-thirds of the Delicious had recovered by February 10. No further recovery was evident by April 25, and about one-fourth of the apples had developed internal breakdown.

All of the Arkansas apples were affected with water-core on October 14, and all of them had completely recovered by March 30.

It will be seen from the various experiments that considerable recovery from water-core can be expected during storage. With firm long-keeping varieties such as the Winesap and Arkansas the recovery has usually been fairly complete, with little complication with other troubles; but with Jonathan, Delicious, Stayman Winesap, and Rome Beauty, water-core has been somewhat more persistent, and recovery has often been accompanied or followed by internal

breakdown. Small-sized apples made a better recovery than the larger ones. The recovery from water-core was almost as complete in commercial cold storage as in air-cooled storage.

SUMMARY

Irrigation experiments have been conducted for a period of six years. Apples from lightly irrigated trees developed more water-core than those from heavily irrigated trees, and apples from trees receiving heavy irrigation followed by light usually had more water-core than those from trees receiving light irrigation followed by heavy. An excess of soil moisture late in the season showed no tendency to increase the amount of water-core.

Apples from trees receiving nitrate or potash fertilizers usually had less water-core than those from untreated trees.

Large apples showed a greater susceptibility to water-core than smaller ones, but increasing the size of the apples by irrigating or fertilizing did not increase the percentage of apples affected by water-core.

Apples that were freely exposed to sunlight showed a strong tendency to water-core, while those that were somewhat shaded were usually entirely free from the disease, except in very late pickings. Sunburned apples were extremely susceptible to water-core.

Water-core increased rapidly as the apples became over-mature.

Picking at the proper stage of maturity is the most practicable preventive now known for the disease.

There was a close correlation between sap concentration and water-core. Heavy irrigation tended to decrease both sap concentration and water-core. Exposed and sunburned apples had a very high sap concentration and were very susceptible to water-core. The exposed sides of apples had a higher sap concentration than the shaded sides, and were more susceptible to water-core. Water-core apples had a higher sap concentration than normal apples, and the water-core tissue of an apple had a higher sap concentration than the sound tissue of the same apple. Sap concentration increased with the maturity of the apples, but apples that were sunburned or water-cored early in the season had a higher sap concentration at that time than normal apples ever attained even if left on the tree several weeks after the usual picking season.

Water-cored and sunburned apples had a lower acidity than normal apples.

Water-core is apparently the result of sap exudation under pressure. The present evidence seems to point to high sap concentration as a precursor of the disease, and the writers are of the opinion that it is much more responsible for the occurrence of water-core than variations in rainfall or soil moisture.

The small-sized apples made better recovery in storage than the larger ones. The kind of wrapper had little or no effect upon the extent of recovery. In most cases the recovery was practically as complete in cold storage as in air-cooled storage. Arkansas and Winesap apples made a better recovery than Stayman Winesap, Rome Beauty, Delicious, or Jonathan. Water-core apples had a high degree of susceptibility to internal breakdown.

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PLATYGASTER HIEMALIS FORBES, A PARASITE OF THE HESSIAN FLY [1]

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INTRODUCTION

One of the most widespread and effective natural enemies of the Hessian fly (*Phytophaga destructor* Say) in the United States is the serphoid parasite *Platygaster hiemalis* Forbes.[3] Although it has been recognized as an important parasite since 1841, when Herrick (*1*)[4] made some initial observations on what was evidently this insect, yet until recent years the species has been confused with at least one other serphoid parasite of the Hessian fly, and little has been known of its early stages and life history. It is, therefore, the purpose of this paper to present a general biological account of this parasite with records of its economic importance and seasonal history in the East.[5]

ECONOMIC IMPORTANCE

Platygaster hiemalis may be ranked first in importance as a parasitic enemy of the Hessian fly in the Middle Atlantic States. Its closest competitor is the serphoid parasite *Platygaster vernalis* (Myers) which attacks the spring generation of the fly. Estimates show that the latter parasite takes a toll of about 4 per cent fewer flies for the spring generation than does *P. hiemalis* for the fall generation. *P. hiemalis*, moreover, is the only parasite that attacks the fall generation to any appreciable extent, and is therefore of special value in helping to control this generation of the Hessian fly, which would otherwise develop practically unchecked by parasites.

Data obtained during the nine years from 1914 to 1922 show an annual parasitism of the fall generation of the Hessian fly of from 16 to 40 per cent with a yearly average of 28 per cent. Table I gives the percentage of parasitism and the number of hosts examined during the period. In obtaining these data, 48 different localities were visited, many of them during consecutive years. These places were widely distributed and ranged from Montoursville, Pa., on the north, to Staunton, Va., on the south.

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[2] The writer wishes to express his appreciation to W. R. Walton for the interest shown in the preparation of this paper; to H. D. Smith, to the late P. R. Myers, and the late W. R. McConnell for much of the survey work and assistance in rearing, dissecting, and determining the material used; to P R. Myers and R. W. Leiby for helpful criticisms; to R. M. Fouts for the determination of many of the parasites; and to Esther Hastings Hart for the dorsal-view drawing of the adult, adult head, and antennae.

[3] Order Hymenoptera, superfamily Serphoidea.

[4] Reference is made by number (italic) to "Literature cited," p. 275.

[5] For the historical review and bibliography of this species reference should be made to an account of this parasite published by the writer (*8*) in 1922.

TABLE I.—*Percentage of Hessian flies killed by Platygaster hiemalis for each of the years from 1914 to 1922 and the number of hosts examined for each year*

Year	Percentage of hosts parasitized by P. hiemalis	Number of hosts examined	Year	Percentage of hosts parasitized by P. hiemalis	Number of hosts examined
1914	34	1,417	1920	32	2,207
1915	36	355	1921	19	944
1916	16	1,592	1922	17	3,617
1917	40	1,430			
1918	24	1,341	1914–1922	28	15,550
1919	35	2,647			

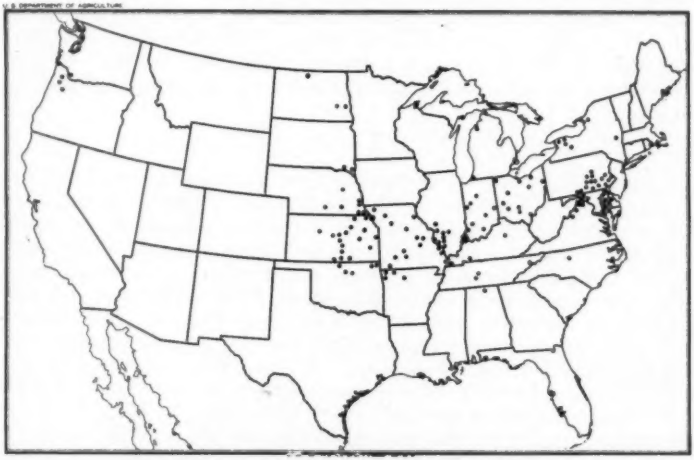

FIG. 1.—Geographical distribution of *Platygaster hiemalis*

GEOGRAPHICAL DISTRIBUTION

Platygaster hiemalis has been found in most wheat-growing regions where the Hessian fly occurs. On the Pacific coast it is present in Washington and Oregon, but C. M. Packard reports that none have been recovered in California. Several years ago it was introduced both into Washington (*12*) and California (*11*), but evidently it has failed to become established in the latter State. The accompanying map (fig. 1) shows the distribution in the United States of localities by counties where *P. hiemalis* has been recovered.[6]

THE EMBRYO

DESCRIPTION OF THE EGG

The egg (fig. 2, A) [7] is highly refractive, subellipsoidal, and slightly flattened along one side. Specimens examined before oviposition

[6] Many of the distribution records were secured through the courtesy of J. R. Horton, A. F. Satterthwait, C. N. Ainslie, and L. P. Rockwood.

[7] The letters used in referring to the figures are: *d*, Discoidal body; *em*, embryo; *g*, gonad; *go*, gorgerette; *ht*, host tissue; *m*, mid-intestine; *md*, mandible; *mo*, mouth; *os*, orifice of salivary glands; *ov*, ovary; *ovi*, oviduct; *p*, paranuclear mass; *pr*, proctodaeum; *s*, salivary glands; *sh*, sheath; *sp*, spermatheca; *spr*, spiracle; *styl*, stylet; *tr*, trophamnium; *v*, vagina.

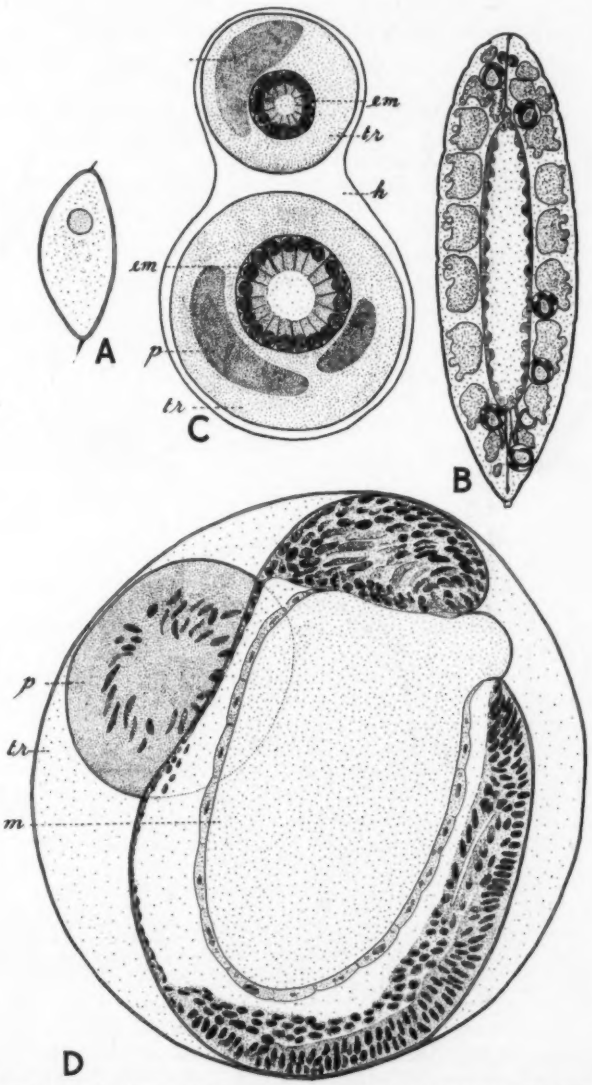

FIG. 2.—A, egg of *P. hiemalis* immediately after oviposition. × 1111. B, host larva containing six *P. hiemalis* embryos. × 18. C, section of embryos at blastula stage of development surrounded by trophamnium and host tissue, and showing paranuclear masses. × 402. D, embryo 18 weeks old surrounded by trophamnium and showing paranuclear mass. × 172.

showed one and sometimes two flagellum-like adherences at one end and one at the opposite extremity. Freshly deposited eggs measure approximately 0.02 mm. long by 0.01 mm. wide. The size and shape of the egg undergo no appreciable change upon oviposition.

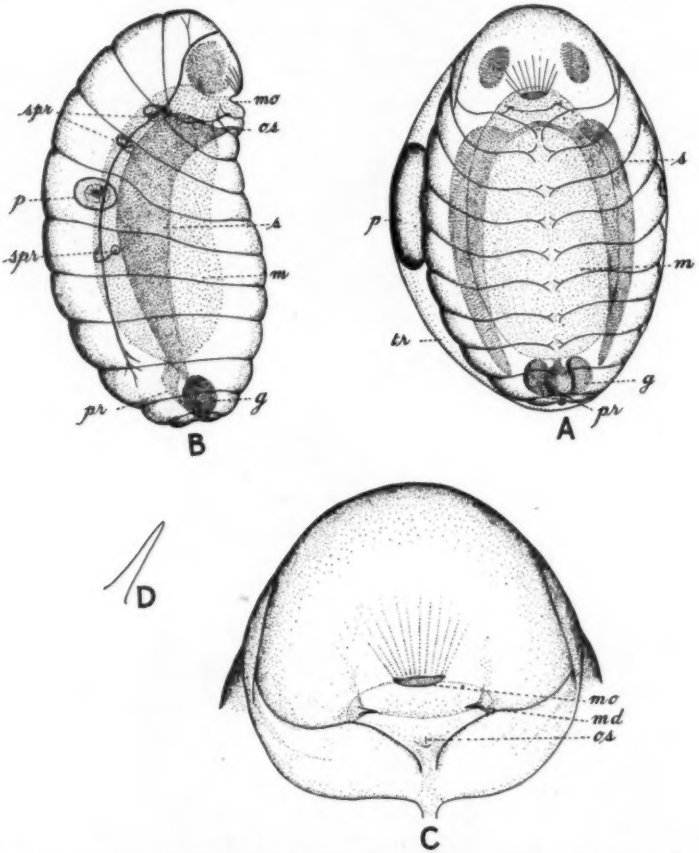

FIG. 3.—A, ventral aspect of *P. hiemalis* embryo nearly ready to break away as a free larva from the surrounding trophamnium. Observe presence of salivary glands, mid-intestine, and gonads. × 60½. B, lateral aspect of larva showing spiracles, discoidal body, salivary gland on one side, mid-intestine, gonad on one side, and proctodaeum. × 45. C, ventral aspect of head of larva showing mouth, mandibles, and orifice of salivary glands. × 97. D, mandible of larva. × 450

EMBRYONIC DEVELOPMENT

Development takes place both polyembryonically and monembryonically in the body cavity of the host (fig. 2, B). In its polyembryonic type of development two embryos are produced from a single egg (fig. 2, C). Shortly after growth commences large paranuclear masses are formed which function as nutritive bodies (fig. 2, C, *p*). The egg also becomes encysted with host tissue (fig. 2, C, *ht*), which serves as the source of supply for the necessary nutrition. Aborted

eggs are frequently found, and this is probably accounted for by the lack of sufficient encysting host tissue. Most of the young embryos separate one from the other at a very early stage of development, but occasionally they are held together by host tissue until quite far advanced in life.[5]

The winter and part of the spring and summer are usually passed in a resting stage (fig. 2, D), in which well-defined larval characteristics are present. Body segmentation is not yet apparent, but the body walls and stomach wall have formed, the buccal cavity has developed, and the proctodaeum is very distinct. More rarely the winter is passed in embryonic forms no further advanced than the blastula stage, and sometimes, on the other hand, in forms sufficiently far advanced to show body segmentation. Such digressions may be attributed to exceptional meteorological conditions or very early or very late oviposition. For instance, in eastern Pennsylvania, during the fall of 1922, emergence of both parasites and hosts was greatly retarded, and cold weather appeared before a majority of the parasites had developed beyond the blastula stage, with the result that most of the *hiemalis* in this region passed the winter in the blastula stage of development.

With the warm weather of summer growth is resumed; whereupon the body lengthens, the segments become distinct, and the trophamnium shrinks. (Fig. 3, A). When the larva is completely formed, it breaks away from the surrounding trophamnium and commences at once to feed.

THE LARVA

The fully developed larva (fig. 3, B) is about 1.4 mm. long by 0.6 mm. in diameter and has seven abdominal and three thoracic segments well defined by sutural lines. It is white, ovoid, bare of setae, with spiracles (fig.3, B, *spr*) present on the second and third thoracic segments, and second abdominal segment. In the first abdominal segment, instead of an external spiracle, there is a large discoidal body (fig. 3, B, *d*) under the cuticula at the terminus of the lateral tracheal branch of this segment. The mouth (fig. 3, C, *mo*) is a simple transverse orifice capable of being opened and closed by strong radiating muscles attached to the superior lip. The mandibles (fig. 3, C, *md*, D) are 0.03 mm. long, attenuated, and nearly straight, a very slight curve only being distinguishable along one plane under high magnification. Large tapering salivary glands (fig. 3, A, B, *s*) extend nearly the full length of the body on each side and unite in a single opening a short distance below the mouth. The mid-intestine (fig. 3, A, B, *m*) is sacklike, and when distended fills most of the contents of the larva. It comes in contact with the walls of the proctodaeum (fig. 3, A, B, *pr*), but no opening from the one into the other is discernible. The external orifice of the proctodaeum is present close to the ventral edge of the seventh abdominal segment. Gonads (fig. 3, A, B, *g*) are distinguishable on either side of the proctodaeum.

The larva increases somewhat in size as it feeds and the fat bodies develop, but apparently it undergoes no molt, and the mandibles

[5] For a more detailed account of the embryological development of *P. hiemalis* see "The Twinning and Monembryonic Development of *Platygaster hiemalis*, a Parasite of the Hessian Fly," by R. W. Leiby and C. C. Hill (*5*).

remain unchanged in size and shape throughout the period. During this stage all of the contents of the host are consumed except the outer integument and some of the interior of a chitinous nature.

THE COCOON

Before pupating each parasite larva forms an ovoid yellowish-brown cocoon made of a tough, elastic material. When all of the individuals within a single host have developed to this point, the host skin and puparium become completely filled out by the inclosed parasite cocoons (fig. 4, A).

THE PUPA

The pupa (fig. 4, B), which at first is white, gradually darkens until it is shiny black, with the exception of the integuments between the abdominal plates, which remain white. The scutellum is prominent. The wing pads extend caudad to about the middle of the abdomen, and the antennae reach to within a short distance of the extremity of the wing pads.

COMPARISON OF THE LARVAL FORMS OF PLATYGASTER HIEMALIS WITH THOSE OF OTHER SPECIES IN THE SAME GENUS

As a guide to the identification of the immature stages of this parasite, it is of interest to compare its larval stage with those of some of the other species of the genus Platygaster.

Compared with *Platygaster vernalis*, reared from the same species of host insect, the writer (*3*) has noted a radical difference. *Vernalis* passes through a primary larval stage somewhat resembling a cyclopean form, but in *hiemalis* no larval stage of this sort occurs either in its embryological or larval development. A closer resemblance is found, however, in the final larval stages, although there are still some marked differences. In *vernalis*, maxillae are present and the mandibles are distinctly curved; in *hiemalis* there are no maxillae and the mandibles are nearly straight. Moreover, there are eight segments apparent in the abdomen of *vernalis* and but seven in *hiemalis*.

The same comparisons apply to (*Polygnotus*) *Platygaster minutus* Lindemann, which has been reared from the Hessian fly in Europe and studied by Marchal (*6*), except that Marchal does not mention the presence of maxillae in *minutus*, and finds nine abdominal segments instead of eight.[9]

Two other Platygaster parasites differ radically from *P. hiemalis* in their larval stages: *Platygaster lineatus* Kieffer, a parasite of *Diplosis pyrivora* Riley, and *Platygaster marchali* Kieffer, reared from *Perrisia ulmariae* Br. According to Marchal both have primary larval stages resembling cyclopean forms, thus affording at once a marked distinction in larval development from that of *hiemalis*.

[9] Both *Platygaster vernalis* (Myers) and the parasite studied by Marchal under the name of *Polygnotus minutus* (Lindemann) occur in the same species of host (*Phytophaga destructor*), and very closely resemble each other in all phases of their development; and as Myers (*3*) has pointed out, both may prove to be *Platygaster zosine* Walker.

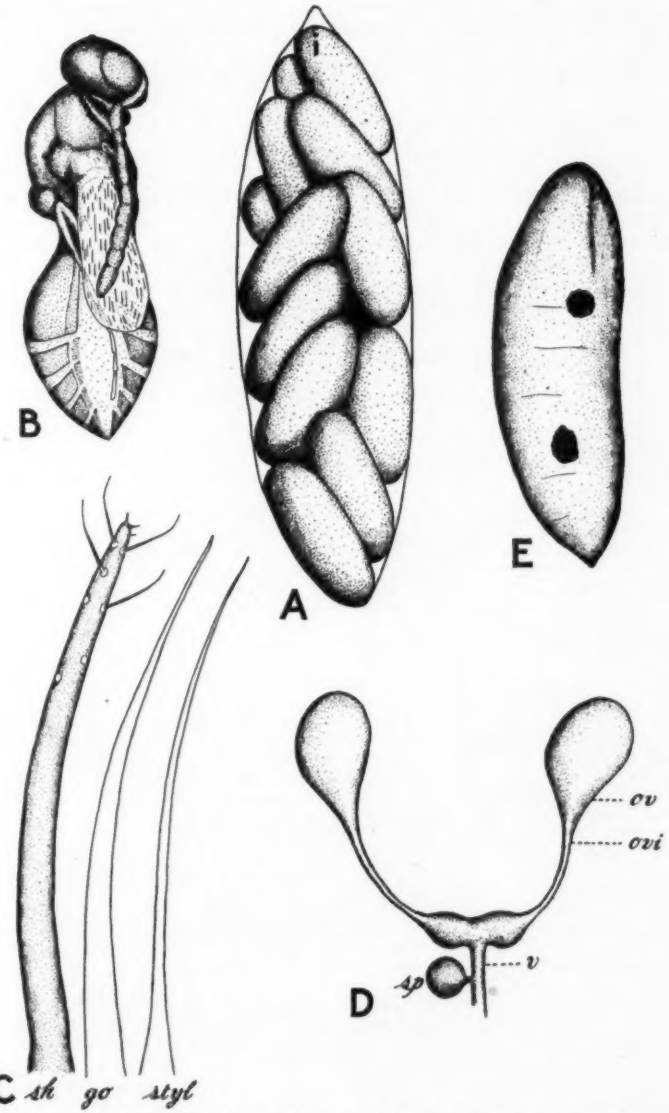

FIG. 4.—A, cocoons of *P. hiemalis* in host puparium. The host puparium is indicated by outline. × 19½. B, pupa. × 43½. C, ovipositor, showing sheath, gorgerette, and stylet. × 572. D, female reproductive system. × 123. E, host puparium, showing exit holes made by adult of *P. hiemalis*. × 14

Compared with *Platygaster herrickii* Packard, another parasite of the Hessian fly, the same outstanding difference is observed in so far as a true cyclopean form is found in this parasite.[10]

Platygaster ornatus Kieffer reared from *Perrisia ulmariae* Br. and depicted by Marchal (*7*) bears, however, a marked resemblance in larval form to *hiemalis*. It shows no distinct secondary larval stage, and the larva is very similar in structure to that of *hiemalis*. *Ornatus*, however, shows traces of maxillae which are lacking in *hiemalis*.

The resemblance of the larva of *hiemalis* and *Platygaster dryomyiae* Silvestri depicted by Silvestri (*10*) and found as a parasite of *Dryomyia lichtensteinii* Fr. Löw is yet more marked. The position and appearance of various essential parts of the anatomy are very similar. In *dryomyiae* traces of maxillae seem to be lacking, as in the case of *hiemalis*. One mark of distinction is in the discoidal body on the first abdominal segment, which appears to be more prominent in *dryomyiae*.

DESCRIPTION OF ADULT[11]

(Fig. 5, A, B, C, D, E, and fig. 4, C)

Female.—Length 0.8 mm. to 1.3 mm.; black and shining; head about twice as broad as long; vertex posteriorly finely regulose; face shining, with very faint aciculations running obliquely downward from a faint median elevation; lateral ocelli equidistant from eye and median ocellus; mandibles fusco-testaceous; antennae 10-jointed, fusco-piceous; flagel twice as long as the scape; scape pale testaceous at base; pedicel as long as the first two flagellar joints, thicker than the second joint; first flagellar joint small, slightly longer than thick, pale testaceous basally; second longer and slightly larger than the third; flagellar joints five, six, seven, and eight each with a pale spur near apex (under compound microscope); club five-jointed, joints except last slightly longer than wide, the last one-half longer than the preceding; pronotum shining, villose, and faintly aciculated; mesonotum shining, villose, and faintly aciculated, slightly elevated medially on the posterior margin; notauli faintly indicated, terminating posteriorly in aciculated, pilose foveae; scutellum highly elevated, convex, distinctly broader than long, immargined laterally; mesopleurae smooth, polished, and bare; propodeum with two median carinae, pilose except in sulcus; metapleurae clothed with dense, silvery pile; anterior coxae fuscous, median and posterior fusco-piceous; anterior trochanters fusco-testaceous, median and posterior fuscous; femora, fuscous, except apex of anterior which are fusco-testaceous; tibiae fuscous except anterior and base of median of posterior, which are fusco-testaceous; tarsi fulvous, anterior lighter than median and posterior; all apical tarsal joints fuscous; wings hyaline, pubescent, about twice as long as the abdomen; petiole dorsally coarsely aciculated; second segment occupying about two-thirds of the dorsal abdominal surface, smooth and polished, with two foveae at base; area between and about these foveae aciculated; remaining abdominal segments each with a row of hairs; ovipositor curved and attenuated, with a few setae at apex.

Male.—Essentially the same as female, but may be distinguished by the second flagellar joint of the antenna, which is thickened and curved, as long as pedicel; spurs on flagellar joints five, six, seven, and eight absent; club six-jointed.

[10] Kulagin (*4*) described two platygasters as having cyclopean forms, but the author fails to find in the account sufficient justification for their determination as platygasters. Furthermore, the cyclopean form depicted by Kulagin as *Platygaster herrickii* not only was taken from a host from which *herrickii* adults have never been reared, but also compares very unfavorably with similar stages which the author has on hand, reared under controlled conditions from *herrickii* adults by the late W. R. McConnell.

[11] Redescribed for this paper by P. R. Myers.

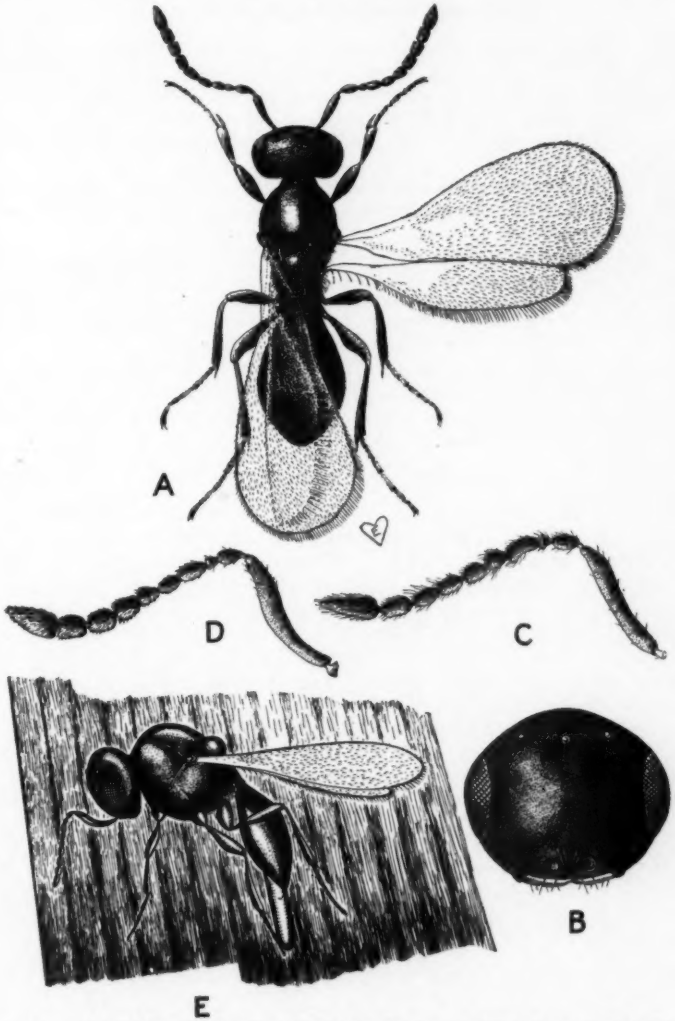

FIG. 5.—A, adult female; B, frontal view of head of adult; C, antenna of male; D, antenna of female; E, female ovipositing into Hessian fly egg on wheat leaf. All greatly enlarged

FEMALE REPRODUCTIVE SYSTEM

(Fig. 4, D)

The ovaries are ovoid, and sometimes, when distended with eggs, considerably elongated. The oviducts are slender and usually slightly longer than the ovaries and open into a two-lobed pouch at the base of the vagina. The spermatheca is spherical and is connected by a small neck close to the base of the vagina.

CERTAIN HABITS AND REACTIONS

The adults are very active and fly readily. When greatly disturbed they feign death. They will lap up water and the juices of a wheat leaf which has been bruised or broken, and will nip at the short pubescence on the wheat leaf. They show no tendency, however, to feed in any way on the host. They are positively phototrophic.

C. N. Ainslie, in unpublished notes on the nocturnal habits of some adults of this species which he had in confinement, made the following observations:

> As darkness came on they betook themselves to the shelter afforded by the groove on the wheat blade and there spent the night, hunched together in a compact fashion, the antennae folded down and the legs bunched. A strong electric light flashed on them at short range and held steadily near them failed to disturb them in the slightest. They were evidently fast asleep.

At the time of eclosion they bite a round or irregularly shaped exit hole through the cocoon and puparium (fig. 4, E). A few such holes in the host puparium usually suffice to permit all the adults within the host to escape.

LENGTH OF LIFE OF ADULT

In order to secure data on the duration of the adult stage, 120 females and 66 males were distributed into three lots and subjected to different conditions. Lot 1 included 28 females and 14 males placed without nourishment in small vials plugged with cotton and exposed to the air in the laboratory in a dry condition. Lot 2 contained 58 females and 34 males in small vials plugged with cotton, the plugged ends of which were inserted in a plaster block kept constantly saturated with water. The cotton absorbed sufficient moisture from the plaster block to supply water for ingestion. Lot 3 consisted of 34 females and 18 males kept in a saturated atmosphere in the same manner as lot 2, but provided with sugar solution for nourishment. The results are summarized in Table II. It will be seen that the greatest length of life was 18 days and 19 hours; that in each lot the average length of life of the female exceeded that of the male; and that the parasites left in a saturated atmosphere with sugar solution for nourishment had the longest average length of life, which amounted to 11 days 2 hours. The entire experiment was conducted under ordinary laboratory temperature which varied from 51° to 78° F., with an average temperature of 66° F.

TABLE II.—*Length of life of Platygaster hiemalis adults*

[Lot 1 was kept in a dry atmosphere with no nourishment accessible; lot 2 in a saturated atmosphere with water accessible for ingestion; and lot 3 in a saturated atmosphere with sugar solution for nourishment]

Lot No.	Female					Male					Total average longevity	
	Number used	Longevity				Number used	Longevity					
		Maximum		Average			Maximum		Average			
		Days	*Hours*	*Days*	*Hours*		*Days*	*Hours*	*Days*	*Hours*	*Days*	*Hours*
1	28	3	20	2	11	14	3	20	2	4	2	8
2	58	8	17	4	22	34	7	20	3	16	4	11
3	34	18	19	11	21	18	17	17	9	15	11	2

PARTHENOGENESIS

Various stages of *Platygaster hiemalis* were reared by the author under controlled conditions from unfertilized females, giving positive evidence of the ability of this species to develop parthenogenetically. It has also been observed from sectioned material that an impregnated female will deposit both fertilized and unfertilized eggs at a single oviposition.

SEX RATIO

From 8,476 adult *Platygaster hiemalis* reared in confinement from Hessian fly puparia collected in the field, 66 per cent were females and 34 per cent males. In a majority of cases both sexes developed in the same host, which may be accounted for by the occurrence of both fertilized and unfertilized eggs.

In this connection it is interesting to note that the percentage of females is considerably lower than Patterson (*9*) found for *Platygaster feltii* Fouts. In the latter species the percentage of females amounted to about 86, as compared with 66 in *P. hiemalis*. In the case of *P. vernalis*, however, the author (*3*) found that the percentage of males somewhat exceeded that of the females, the number of females being a little less than 49 per cent.

OVIPOSITION

Platygaster hiemalis oviposits in the eggs of the Hessian fly (fig. 5, E). The host eggs are cylindrical, and from 0.4 to 0.5 mm. long, and usually are found scattered over the upper surface of the leaves of the wheat plants.

When searching for Hessian fly eggs the parasite keeps her antennae vibrating rapidly against the surface of the leaf on which she is crawling, and swings her head slightly from side to side in order apparently to cover more area with her antennae. As soon as she identifies an egg she halts and with an increased rapidity of motion of her antennae, concentrates on the spot. Sometimes she seems to lose track of the egg for a moment, but when this happens she usually turns in small circles until she finds it again. When the egg is located she strokes it rapidly for a second or two with both antennae, and if satisfied with this preliminary examination, quickly draws up her abdomen so that the tip of the ovipositor touches the surface of the egg. At the same time she swings her body at right angles to its long axis and places the tarsi of the middle legs just beyond the ends of the egg. Thus poised, and with antennae held motionless in a downward position, she hurriedly slides the tip of her ovipositor from one end of the egg to the other as if to make sure of its position and character. If all is well she brings her ovipositor to a halt at about the middle of the egg and commences to insert it. In no case did the author see more than a small fraction of the length of the ovipositor inserted. The entire process from the time the parasite first locates the egg until the ovipositor is withdrawn requires about 45 seconds.

It is evident from the manner in which the female uses her antennae and ovipositor in the process of finding the host egg and ovipositing, that tactile reactions take place to a large extent. The author, however, has frequently observed the females of this species stop and

examine with their antennae the place on a wheat leaf from which a host egg had been removed, and even attempt to oviposit on such a spot. This appears to be a very evident case of chemotropism, and undoubtedly reaction of this kind plays an important rôle in the location of the host egg.

This species also shows a marked ability to recognize eggs in which it has once oviposited, and when retracing its course over a number of host eggs avoids piercing a majority of those previously attacked. In one instance a female, crawling over a leaf which bore 42 eggs, oviposited in 24 of them in fairly regular order on the first trip. On the return trip, however, two that had not previously been pierced were attacked, and only one that had been visited previously was pierced a second time, although she brushed them all with her antennae. In another case, 9 out of 11 eggs were pierced on a first visit, and on a second inspection of the same eggs only the two that had not been attacked before were selected. A. L. Ford, in unpublished bureau notes, recorded similar observations on 5 different females of this species. He noticed that on a return trip over an egg-strewn leaf they carefully examined all the eggs with their antennae, but only oviposited in those which had been overlooked on the first trip; and only after all the eggs had been punctured did he observe them pierce a host egg more than once. He also mentioned the fact that one female did not seem able to recognize the occurrence of oviposition by another female. C. N. Ainslie observed similar behavior in two females of this species which he had in confinement. He said:

> The two Polygnoti in the tube worked steadily for hours, attacking the eggs on the wheat blades, inspecting every egg they approached. Never, as near as I could judge, was the same egg attacked more than once, even under these abnormal conditions.

The number of eggs laid at a single oviposition varies from 1 to 8. From the examination of 81 hosts pierced by *Platygaster hiemalis* while held under observation under a binocular microscope, the author found an average of 4.22 eggs laid per deposition. This figure is conservative, owing to the difficulty in always recovering all the eggs laid.

PROLIFERATION

It has been shown by Leiby and Hill (*5*) that, in addition to the twinning and monembryonic development of this parasite in certain of the earlier stages, the parasites sometimes become aborted and pseudoforms are developed. In order, therefore, to calculate the effects of twinning and abortion in the proliferation of this insect, special observations were made. Facts justify the assumption that host eggs are seldom oviposited into more than once. Many hosts were collected from divers localities and records kept of the number of *Platygaster hiemalis* embryos found in each. Since it has been shown that the phenomena of twinning and abortion in embryo development occur very early in the growth of the parasite, the embryos observed at the time of examination had passed beyond the twinning stage. The abortion period likewise was past and the early cases of aborted eggs were not included in the records. Thus the figures obtained represent with considerable accuracy the number of developing embryos resulting from an average oviposition. Hosts

to the number of 2,220 were collected and dissected and an average of 7 embryos per host was found. Thus 7 healthy embryos may be assumed to develop from a single oviposition. The average number of adults, however, that succeed in emerging from a host was found to be 6.31 (*2*). This is slightly less than the number of embryos which develop, and shows a mortality of about 0.69 per host between the period from embryo to adult. In consideration of the fact that an average of 4.22 eggs are laid per deposition, it results that adults develop at the rate of 1.5 per egg.

Some latitude should be allowed for individual variation. The number of adults to emerge from a host was found to range from 1 to 16, and as many as 23 fully formed *hiemalis* cocoons have been found in a single host carcass.

The greatest total number of ovipositions made under the author's observation by an individual *Platygaster hiemalis* in confinement amounted to 160. These were all deposited in the course of 24 hours and there is no reason to believe that if sufficient host material had been available there would not have been many more laid. C. N. Ainslie reported observing one female of this species oviposit uninterruptedly on four successive days. At the rate of 4.22 eggs per oviposition there must have been a total of slightly over 675 eggs laid in the course of 160 ovipositions, which would have produced under normal conditions more than 1,000 adults.

POTENTIAL PROGENITIVENESS

In order to ascertain the full egg-laying capacity of *Platygaster hiemalis*, the ova contained in the ovaries of 10 individuals were dissected out and counted. (In this species the ova found in the adult stage are fully developed in size at the time of eclosion.) The results showed a maximum number of ova per individual of 6,336, a minimum of 1,675, and an average of 3,322. More eggs were sometimes found in one ovary than in the other of the same individual; the largest number found in any single ovary amounted to 3,671.[12] Assuming, therefore, that adults would develop at the rate of 1.5 per egg as figured above, the progeny from an average female, if she oviposited to her full capacity, would come to 4,983 adults. Deducting from this figure the 34 per cent which will develop into males, we have left a total of 3,289 females with the capacity of producing 20,819 adults [3,289×4.22 (eggs per ♀)×1.5 (adults per egg)] for the following generation.

SEASONAL HISTORY

Throughout most of the eastern wheat-growing region of the United States *Platygaster hiemalis* has but one generation a year. The adults emerge in the fall, during the egg-laying period of the Hessian fly. They at once oviposit in the eggs of their host, and the embryos develop until cold weather sets in, causing them to remain dormant in this stage until the advent of warm weather late in the

[12] In counting these eggs a very high degree of accuracy was made possible by spreading the eggs from one ovary at a time over an ocular micrometer disc ruled into 1 mm. squares. In 1909 C. N. Ainslie dissected out both ovaries from a female of this species, broke them in water under a cover glass, and counted them through a high-power microscope. Two hours were spent in making an accurate count and the total number found came to about 3,600. The record, however, was never published. It will be observed that this count is very close to the average number of eggs found by the author.

spring. Although individuals sometimes pass the winter as very young embryos or as embryos considerably advanced in growth, the vast majority reach and remain at a certain point of development (fig. 2, D) characteristic of the hibernating stage of this species. This stage of growth has become so adapted to the habit of dormancy that such embryos are frequently encountered through the summer months. Most of them develop into free-living larvae during June and July. The contents of the host is then consumed and cocoons are formed. By the end of August most of the larvae have pupated and transformed into adults within their cocoons, where they remain until weather conditions are suitable for emergence and egg laying. Stray adults are occasionally found much earlier in the year, a fact which would indicate that precocious development sometimes takes place. In the spring-wheat region of northern New York the seasonal history of *P. hiemalis* is greatly modified and we find many adults emerging in the spring, which enables them to take advantage of the principal egg-laying period of their host in this region. Similar modifications in the seasonal history may occur in other parts of the United States where climatic conditions vary from those in the East. Figure 6

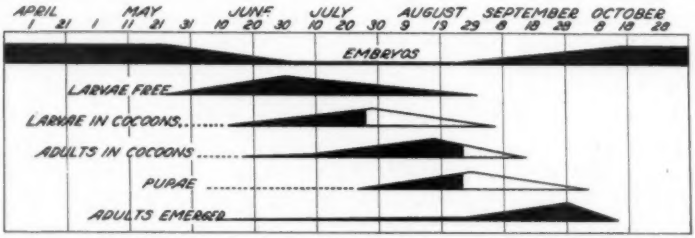

FIG. 6.—Diagram illustrating the seasonal history of *Platygaster hiemalis* in the vicinity of Carlisle, Pa. Dark areas show periods of occurrence and relative abundance of the various stages of life history as found by field observations. Light areas and dotted lines indicate probable occurrence of such stages

shows the average seasonal growth of the various stages of this parasite, based on data obtained in the vicinity of Carlisle, Pa., during the years 1918 to 1923, inclusive.

SUMMARY

Platygaster hiemalis is one of the most widespread and effective parasites of the Hessian fly in the United States. In the eastern wheat-growing regions it kills annually from 16 to 40 per cent of the fall generation of the fly, with an average yearly toll of 28 per cent.

The eggs are about 0.02 mm. long, subellipsoidal, and highly refractive. They develop polyembryonically by twinning, monembryonically, and some become aborted. The resulting yield in adults is a 50 per cent increase over the number of eggs deposited; and an average of 6 adults emerge from each host.

The larva is about 1 mm. long, and is white, ovoid, and bare of setae. During the larval stage the parasite consumes the contents of the host. Before succumbing to attack, however, the host usually succeeds in forming a darkened puparium.

Before pupating the parasitic larvae form ovoid, yellowish-brown cocoons. These are found packed closely within the cuticula of the host larva inside the host puparium.

The adult, which is about 1 mm. long and shiny black, is very active, flies readily, and is positively phototrophic. The female is able to reproduce parthenogenetically, and impregnated females usually deposit both fertilized and unfertilized eggs at a single oviposition. Approximately 66 per cent of the adults are females. The female deposits her eggs in the eggs of the host, and lays from 1 to 8 eggs at each oviposition. She seldom oviposits more than once in the same host. The ovaries of an average female contain 3,322 eggs.

Throughout most of the East *Platygaster hiemalis* passes the winter and early spring in the embryonic stage. During June and July it develops into free-living larvae, and by the end of August most of these have pupated and transformed into adults, ready to emerge from their cocoons during the oviposition period of the Hessian fly in the fall of the year.

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A BIOLOGICAL STUDY OF CEPHUS PYGMAEUS (LINNAEUS), THE WHEAT-STEM SAWFLY[1]

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INTRODUCTION

During the last few years the wheat growers of New York State have called the attention of entomologists to another exotic insect that has become a wheat pest of economic importance. This insect, "The wheat-stem sawfly" (*Cephus pygmaeus* Linnaeus), has been seriously infesting the wheat of this State, and is now extending its ravages into Pennsylvania. Because of its increasing ravages, this sawfly may come to be nearly as important as the Hessian fly.

The first infestations were recorded in 1887, by J. H. Comstock (*5*) [3] at Ithaca, N. Y. In the same year W. H. Harrington (*9*) reported having collected it while sweeping in a meadow near Ottawa, Canada. C. V. Riley (*12*) reported in 1888 that Harrington received specimens collected by Van Duzee in 1887 near Buffalo, N. Y. The Canadian record by Harrington in 1887 is the only record of this insect in Canada; as far as data are available, no specimens have been collected since that date. In 1892 F. H. Chittenden (*4*), in a short article on the date of introduction of the insect into this country, states that he collected specimens in the vicinity of Ithaca, he thinks, as early as 1882, but owing to the fact that there was no date on the specimens it was difficult to determine the exact time they were collected. Since 1887, this insect has spread very slowly, and is still quite restricted in distribution.

Severe damage to wheat on the Cornell University farm was recorded by J. H. Comstock (*5*) as early as 1887. No reports were received of its injuries from that time until about 1921, when it again became abundant and its work became apparent in the wheat-growing areas of New York State. Since 1921 it has continued to increase in abundance and its ravages to increase in severity.

The present paper, which aims to include a study of the life history and habits of *Cephus pygmaeus*, is based largely on observations made by the writer in 1923 and 1924.

SYNONYMY

According to Linnaeus (*10, p. 929*) this species was first mentioned by Geoffroy (*8, p. 4*) as *Tenthredo species* in 1762, but it was not until five years later, when Linnaeus described the species under

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[3] Reference is made by number (italic) to "Literature cited," p. 294.

the name of *Sirex pygmaeus*, that it was first given a valid specific name.

Following is the complete synonymy of *Cephus pygmaeus*, as understood by the writer:

Tenthredo species Geoffr., 1762, Hist. Abr. Insect. 2: 288, no. 38.
Sirex pygmaeus Lin., 1767, Syst. Nat., Ed. 12, p. 929, no. 7.
Tenthredo longicornis Fourcroy, 1785, Entom. Paris., p. 378.
Banchus spinipes Panz., 1801, Faun. Insect. German. 1: 92.
Cephus pygmaeus Latr., [1802], Hist. Nat. Insect. 3: 303.
Astatus pygmaeus Klug, 1803, Monogr. Siric. German., p. 50, no. 2.
Astatus spinipes Klug, 1803, Monogr. Siric. German., p. 51, no. 3.
Astatus floralis Klug, 1803, Monogr. Siric. German., p. 53, no. 5.
Banchus viridator Fab., 1804, Syst. Piez., p. 127, no. 5.
Pamphilius longicornis Latr., [1805], Hist. Nat. Insect. 13: 140, no. 5.
Cephus spinipes Panz., 1806, Krit. Revis. 2: 144.
Trachelus pygmaeus Jur., 1807, Nouv. Méth. Class. Hyménop. 1: 72.
Cephus Leskii Lepel., 1823, Monogr. Tenthred., p. 20, no. 58.
Cephus atripes Steph., 1835, Illus. Brit. Entom. 7: 105, no. 4.
Cephus floralis Steph., 1835, Illus. Brit. Entom. 7: 106, no. 7.
Tenthredo pygmaeus Blanch., [1849], Cuvier, G., Règne Anim., Ed. [3], [13 (Insect. Texte 2)]: 128.

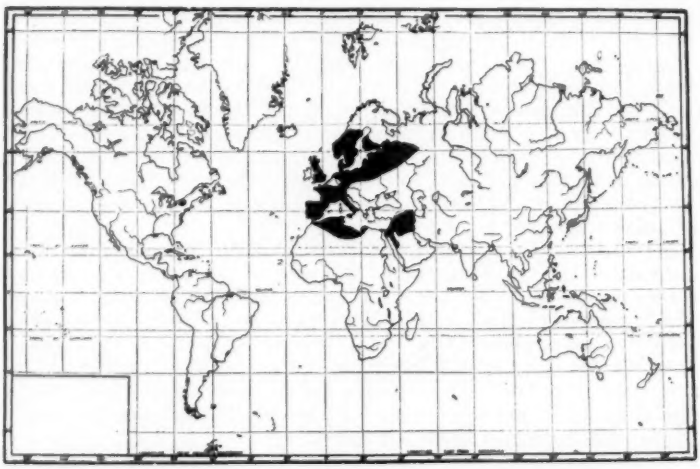

FIG. 1.—Black area indicates present known distribution of *Cephus pygmaeus*

COMMON NAMES

J. H. Comstock (*5*), in his paper published in 1889, terms this insect "A Saw-fly Borer in Wheat." Most investigators writing to-day, however, call it the "Wheat-stem Sawfly Borer." This does not seem to apply exactly to it, since wheat is not the only host plant, although it is probably the most important. P. R. Myers, of Carlisle, Pa., terms it the "Northern Grain-stem Sawfly," and this, in the opinion of the writer, is very appropriate, as it is found infesting a number of grains other than wheat.

DISTRIBUTION

This is an Old World insect, which, according to available records, was first noted in 1762 by Geoffroy (*8, p. 4*) from specimens col-

lected in Sweden. It was soon noted by other writers from different European countries. Linnaeus (*10, p. 929*), in 1767, gave its habitat as Europe. A similarly wide range was ascribed by Cameron (*3, p. 122*) in 1890, and by Dalla Torre (*6, p. 410*) in 1894, but the latter in addition included "boreal" America, while a French writer (*13*) reported *Cephus pygmaeus* as causing great ravages in Northern Africa in 1897.

The present known distribution of this insect in the Old World includes Sweden, Germany, Holland, Switzerland, France, Spain, Italy, Russia, England, Denmark, Norway, North Africa, and Mesopotamia. These are given in chronological order according to the records of the appearance of the insect in them. The map of Figure 1 aims to visualize the approximate world distribution of *Cephus*

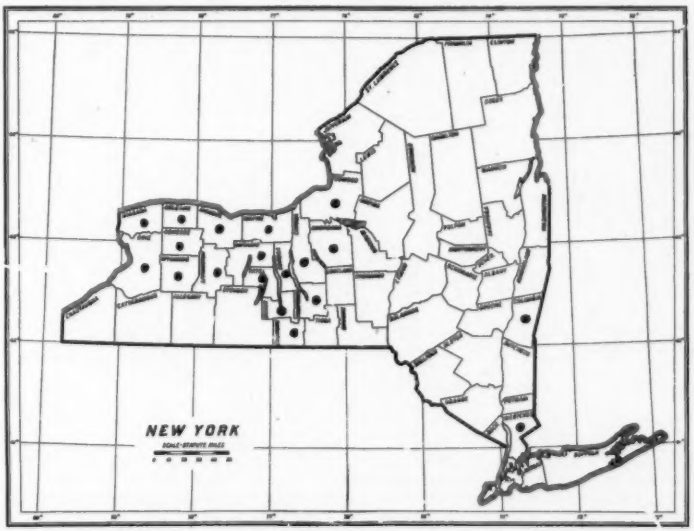

FIG. 2.—Dots indicate counties in New York State where there is infestation by *Cephus pygmaeus*

pygmaeus as understood by the writer. The European range of this insect is very similar to that of the Hessian fly. The Hessian fly is found further east in Persia and Asia Minor than is the sawfly.

The distribution of *Cephus pygmaeus* in the United States is extremely limited. Since its discovery in 1887 in the vicinity of Ithaca, N. Y., and near Buffalo, N. Y., in the same year, it has spread very slowly from these points. Its present range is known to be a restricted area consisting of 20 counties of New York and 14 counties of Pennsylvania.

The range of this sawfly in New York State includes Cayuga, Chemung, Columbia, Erie, Genesee, Livingston, Monroe, Niagara, Onondaga, Ontario, Orleans, Oswego, Schuyler, Seneca, Steuben, Tompkins, Wayne, Westchester, Wyoming, and Yates Counties (fig. 2).

This insect has been recorded from the following counties of Pennsylvania: Bradford, Columbia, Cumberland, Dauphin, Juniata, Lebanon, Lycoming, Montour, Northumberland, Perry, Snyder, Tioga, Union, and York (fig. 3).

Previous to 1924 there seemed to be no connection between the range in New York and that in Pennsylvania, but in that year P. R. Myers and the writer were able to collect larvae of *Cephus pygmaeus* in both Tioga and Bradford Counties, Pa., while the writer found it in material collected by C. R. Crosby in Chemung County, N. Y.

Whether or not it occurs in Ohio and the New England States is still a question. The author has endeavored to solve this problem

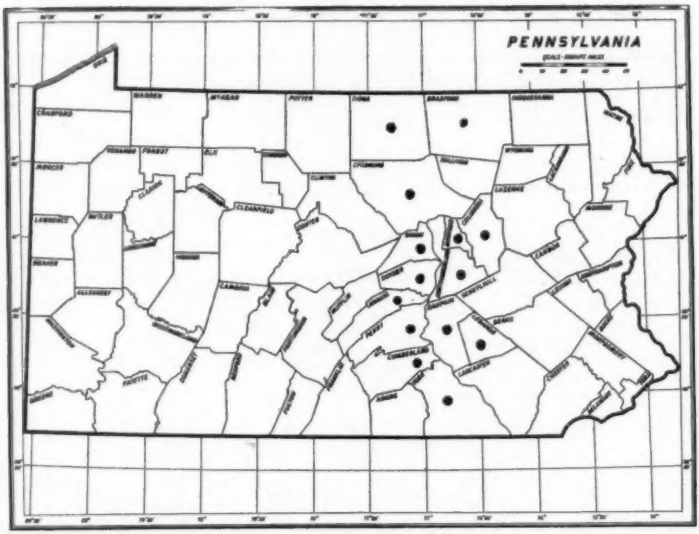

FIG. 3.—Dots indicate counties in Pennsylvania where there is infestation by *Cephus pygmaeus*

through communications with entomologists in those places, but their replies were either negative or doubtful. It is, of course, highly possible that this insect may occur in these regions, but since it has not become plentiful enough, as yet, to become a serious pest, it has not been observed by entomologists or attracted the attention of the farmers.

FOOD PLANTS

The food plants of the grain-stem sawfly are comparatively few. The writer has examined a large number of grains and grasses and found that only certain species were attacked.

The principal food plants are wheat, barley, rye, and a species of chess. Although a large number of fields of oats were examined, in no case was there any evidence of infestation. On several occasions where volunteer rye and barley were growing in a field of oats, the writer found that these plants were nearly always infested, while the oats were free from infestation. Noel (*11, p. 5*), however, reports finding this insect infesting oats in France. A number of Russian

workers, on the other hand, have reported that the sawfly never attacked oats in that country.

In this country, as far as data are available, timothy is free from infestation. A large quantity of this grass that was growing in the vicinity of wheat fields was examined by the writer, but in no case were any larvae or eggs of the sawfly found. Zacher (*14*), however, reports that he has found it infesting meadow grasses in Germany. The writer examined a large number of meadow grasses in 1923, but was unable to find any infestation; although he was able to get females to oviposit in the stems, these eggs never seemed to hatch or reach maturity. In the summer of 1924, however, he found the larvae of the sawfly infesting a grass in two localities in New York State, viz, Orleans and Genesee Counties. This food plant was determined by A. S. Hitchcock of the United States Department of Agriculture as *Bromus secalinus*, Linn. This plant is commonly known as chess or cheat, and is a common weed in grain fields.

Wheat is by far the most important food plant of this insect in the Uniten States, and consequently suffers the greatest injury. In New York and Pennsylvania the winter wheat is the most severely damaged, as there is very little spring wheat grown in these States. Winter wheat also seems to be the principal crop injured in nearly all of the countries where the sawfly is found, although Borodin (*2*) reports that spring wheat is infested more than barley. He also says that the insect developed better in winter wheat plants. The writer has found greater infestation in thinly drilled wheat, where the plants are larger and healthier, than in the fields where the plants are drilled closer together and the stems are smaller.

Rye may be attacked, but the per cent of infestation never runs very high.

The infestation of barley is comparatively slight, although in 1923 the writer found an infestation of 60 per cent in a field of Alpha barley at Batavia, N. Y. The amount of infestation seemed to depend on the proximity of the barley to a field of wheat.

Since the larva of this insect is wholly unable to move from one stem to another, it is obvious that the stem of the host plant must be large enough to supply both food and shelter for it during its growing period. This may explain why only those grains and grasses having large stems are attacked, and why the female usually chooses the largest and healthiest stems of the host plant in which to oviposit. Probably this is the reason that oats and timothy grass are not attacked.

INJURIES AND LOSSES

The injury caused by this insect is not only peculiar and very interesting, but quite characteristic of it as well. Soon after hatching the larva begins to tunnel down through the stem, leaving behind it a trail of frass. When the larva has reached maturity and is ready to form its cocoon, it compacts a mass of frass within its burrow and about 1½ to 2 inches above the ground line. The upper surface of this plug seems to have no definite shape or stopping point, while the lower edge is slightly concaved. Just below this the larva cuts a V-shaped groove completely around the interior of the culm. It does not cut entirely through the culm, but leaves a thin layer of its epidermis uncut. The straw, therefore, does not break over

immediately. Just below this V-shaped cut the larva places another plug. This second plug is concaved very deeply on the upper surface while the lower surface, to which the cocoon is attached, is flat. The accompanying sketch (fig. 4) is a longitudinal section of an infested stubble showing the two plugs together with the groove between them and the larva in its cocoon. Part of the cocoon has been torn away to show the larva within. In the opinion of the writer, the effect of the plugs is to strengthen the stem above and below the cut and thus allow the stem to break off more easily at the point where the cut has been made. The groove, of course, allows the stem to break over when rubbed against, or when blown by a wind, and the larva is thus left safe in its hibernation chamber for the winter. When the straw breaks over, the upper edge of the remaining stub is usually ragged. This ragged condition of the infested stub is characteristic of this species of sawfly.

FIG. 4.—Drawing of wheat stubble, showing injury caused by larva of *Cephus pygmaeus* and larva within the broken cocoon. ×2½

Below the plug the larva spins the cocoon in which it will spend the winter. This cocoon is free from the sides of the stem, but in most cases is attached to the lower surface of the plug. By careful manipulation it may be removed intact from the stem. In the spring the adults are able easily to force their way out through the plug.

The losses caused by severance of the wheat culms by the larvae are very slight, in the opinion of the writer, since most of the farmers to-day rake their grain fields after cutting, thereby saving the "straw-fallen" stems. The writer has gone over a number of infested wheat fields after cutting and examined the stems left on the ground. In most cases the loose stems were not infested and were free from injury by the sawfly.

As to the losses incurred by this insect there are no available data. A number of heads were weighed, but there was a bad infestation of Hessian fly and wheat midge coincident with that of *Cephus pygmaeus* and accurate results could not be obtained. It did seem, however, that in most cases the heads taken from infested plants weighed more than did the heads taken from healthy plants. This may be due to the fact that the female oviposits in the largest and healthiest stems. Comstock (*5*) reached the same conclusions. The tabulation which immediately follows is taken from his work:

	Grams
Bundle No. 1:	
Grain from 99 infested heads weighed	85
Grain from 99 noninfested heads weighed	70
Grain from 99 noninfested heads weighed	77
Grain from 99 noninfested heads weighed	67
Bundle No. 2:	
Grain from 16 infested heads weighed	12. 3
Grain from 16 noninfested heads weighed	11. 3
Grain from 16 noninfested heads weighed	* 13. 6
Grain from 16 noninfested heads weighed	11. 9
Bundle No. 3:	
Grain from 173 infested heads weighed	165
Grain from 173 non-infested heads weighed	140
Grain from 173 noninfested heads weighed	130
Grain from 173 noninfested heads weighed	120

* These were large selected heads.

These figures clearly show that the infested plants produced heavier heads of grain than did the healthy plants. Comstock gives the following explanation of this:

> It seemed to point to the absurd conclusion that the presence of this borer within a stalk increased the amount of grain produced by that stalk. It was noted, however, that the infested stalks were almost invariably large, healthy ones, with good well-filled heads. When we recall the fact that the laying of the eggs takes place while the wheat is still small, and that a stalk must be large enough to contain a hollow of considerable size before it is suitable for the development of a larva, it will be seen that the stalks infested will naturally be those that are the largest early in the season; while the stalks that are backward in their development, and consequently will produce smaller heads, will escape the attack of the insect.

The writer has made similar determinations which check very closely with those given above, but these data were destroyed by fire.

The infestation of this insect runs quite high, and varies greatly with the locality. Although most of the work here reported was done by the writer on the Cornell University farm at Ithaca, N. Y., he also spent considerable time studying the conditions on the experimental plats of a seed company at Batavia, N. Y., and some time in the vicinity of Mount Morris and Avon, N. Y., studying the infestation. In the summer of 1924 he studied conditions in Pennsylvania.

TABLE I.—*Infestation of Cornell University farm, June 18, 1923*

Sample No.	Number of straws	Larvae found	Eggs found	Percentage infestation	Host plant
				Per cent	
1	25	1	3	16	Wheat.
2	25	2	8	40	Do.
3	20	0	3	15	Do.
4	20	0	2	10	Do.
5	20	0	1	5	Do.
6	18	0	2	11	Do.
7	20	1	9	50	Do.
8	20	3	1	40	Do.
9	15	5	0	33	Rye.
10	25	0	0	0	Do.

These infestation data in Table I were recorded early in the season, about two weeks after the first adults had appeared in the field. Many of the eggs had not yet hatched. All the larvae that were found were very small. Although the counts were made early in the season, they show that there is considerable variation in percentage of infestation in the same grain.

During the latter part of July, 1923, after nearly all of the larvae had reached the base of the stems, the writer collected a number of samples on the Cornell University farm. Two linear feet of stubble was collected from each plat. This stubble was carefully dug so that all of it was saved. Of the 10 samples that were collected, 9 were different varieties of wheat, and all were under experimentation by the department of plant breeding of Cornell University. The results of these examinations will be found in Table III.

TABLE II.—*Infestation chart of material collected at Batavia, N. Y., June 26, 1923*

Sample No.	Straws counted	Number infested	Percentage infestation	Host plant	Locality
1	25	1	4	Rye	1 mile northwest of Batavia.
2	25	14	56	Wheat	Do.
3	25	11	44	....do	Do.
4	25	1	4	Rye	Do.
5	25	13	52	Wheat	Do.
6	25	19	76	....do	Do.
7	25	15	60	....do	Do.
8	25	10	40	....do	Do.
9	25	8	32	....do	1½ miles northwest of Batavia.
10	25	0	0	Timothy	Do.
11	25	2	8	Barley	1 mile northwest of Batavia.
12	25	9	26	Wheat	One-half mile northwest of Batavia.
13	25	17	68	....do	1 mile northwest of Batavia.
14	25	10	40	....do	3 miles northwest of Batavia.
15	25	10	40	....do	5 miles northwest of Batavia.
16	25	11	44	....do	South Byron.
17	25	4	16	....do	Batavia city limits, northeast.
18	25	10	40	....do	1¼ miles north of Batavia.
19	25	16	64	Barley	Do.
Average for 19 samples			46		

TABLE III.—*Infestation in different varieties of wheat collected July 28, 1923, on Cornell University farm*

Variety	Number infested	Number not infested	Total number	Percentage infestation
No. 6 Junior	16	26	42	38.09
O. A. C. No. 104	19	40	59	32.2
1185–A1–73–1	14	35	49	28.6
1027–A1–4–7–6	11	34	45	24.44
Honor	14	31	45	31.1
Forward	19	36	55	34.54
Hybrid 86	11	42	53	20.75
1027–A1–8–6–12	24	28	52	46.15
1196–A1–6	7	51	58	12.06
Honor	12	47	59	20.33

It will be noted in Table III that the samples containing a large number of roots per 2 linear feet had a slightly lower percentage of infestation than those samples with fewer roots per 2 linear feet. This, however, does not apply in the case of the variety 1027–A1–8–6–12, where the highest infestation (46.15 per cent) was found. This variety seems to be very susceptible to attack of the sawfly, as at both Ithaca and Batavia the writer found it to be very heavily infested. At Batavia nearly the entire experimental plat was down, and infestation was nearly 90 per cent.

Through the kindness of P. R. Myers the writer was able to obtain the infestation records of *Cephus pygmaeus* for New York State for the years 1921 to 1924, inclusive. The percentages of infestation were obtained from samples of wheat forwarded by C. R. Crosby of Cornell University to the laboratory of the United States Bureau of Entomology at Carlisle, Pa.

The percentages for 1921 and 1922 in Table IV are based on the examination of 75 tillers of wheat; those for 1923 on the examination of 50 to 250 tillers of wheat; while those for 1924, with the exception of two samples, are based upon the examination of 50 tillers. The

large increase in the percentage of infestation during the past few years is not entirely due to the greater abundance of the insect itself, but to a more thorough examination of the wheat samples.

TABLE IV.—*Infestation records of Cephus pygmaeus in New York State*

County	1921		1922		1923		1924	
	Number of samples	Per cent infestation	Number of samples	Per cent infestation	Number of samples	Per cent infestation	Number of samples	Per cent infestation
Cayuga	5	7.20	6	16.00			8	22.00
Chautauqua					4	0.00		
Chemung							2	12.00
Columbia	4	4.76						
Erie	8	.25	8	2.00			5	28.40
Genesee	7	2.57	21	17.26	22	30.04	17	38.35
Livingston	15	4.35	6	10.89	10	20.36	7	34.57
Monroe	8	.75	13	3.73	26	5.00	19	33.89
Niagara	6	1.20	9	3.41			6	12.69
Onondaga			5	10.93			4	32.00
Ontario	11	6.09	10	21.70	18	12.00	22	35.55
Orleans	3	4.00	15	8.68			4	36.00
Oswego			2	7.33			1	8.00
Schuyler							2	41.00
Seneca	6	2.67	7	6.78				
Tompkins	3	.00	5	14.93	13	26.04	6	30.51
Ulster	4	.00						
Wayne	11	1.82	11	7.03	17	10.00	13	26.46
Westchester	1	1.35						
Wyoming	9	3.74	5	10.67	5	3.00	5	30.40
Yates					3	7.00	4	32.00
Total and average	101	2.71	123	10.09	118	12.60	125	28.36

DESCRIPTION

EGG

The egg is a shiny, nearly transparent body, reniform in shape. In size, it varies from 1.05 to 1.19 millimeters in length, and from 0.42 to 0.56 millimeter in maximum width, and from 0.42 to 0.49 millimeter in minimum width. This gives an average length of 1.11 millimeters, an average minimum width of 0.45 millimeter, and an average maximum width of about 0.5 millimeter. (The egg that measured 1.19 by 0.56 millimeters hatched while it was being measured the second time to check the first measurement.) When the egg is first laid it is distinctly crescent-shaped, but after a day or so it assumes the reniform shape. Figure 5 is a photomicrograph taken of the egg in situ on the inside of the wheat stem.

LARVA

When the larva first hatches it is nearly transparent, save the head, and curled in the shape of a U. It soon straightens out and is then 1.75 millimeters long. Its large, brown, chitinous head, which is equipped with large toothed and powerful mandibles, seems to be greatly out of proportion to the rest of the body. The head capsule alone measures about 0.28 millimeter in width. The body of the young larva is small and weak, measuring only 0.17 millimeter in width. The internal organs are clearly visible when it first leaves the egg. It is footless, the position of the legs being marked by small rounded tubercles, each of which terminates in a few short bristles which are present in this first instar.

The only means of locomotion which the larva has are the strong caudal horn and mandibles. The horn is brown and equipped with a series of stout bristles near the base. By means of this horn the larva is able to work its way up and down the stem by alternately lengthening and shortening its body. In ascending the stem the caudal horn is thrust against the inside of the stem, the body is straightened, the mandibles then catch hold of the stem wall, and the process is repeated until the larva has reached the desired point.

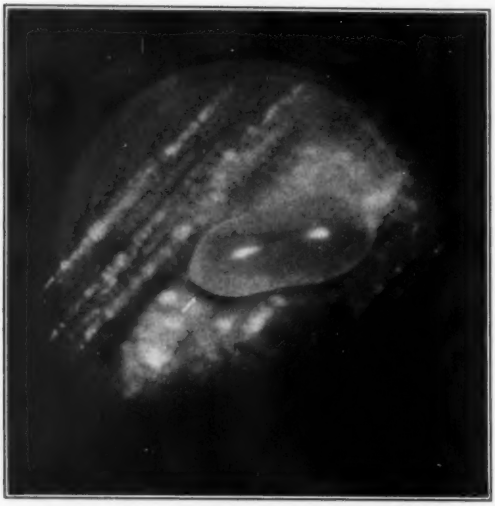

FIG. 5.—Egg of *Cephus pygmaeus*. Much enlarged.

As the larva becomes older and more mature it takes on a color more nearly like that of its food, viz, a yellowish-green. When full grown it measures from 10 to 14 millimeters in length, its size varying with the size of the stem and the amount of the food supply. It becomes shorter, however, after it has spun its cocoon, being reduced to 6 to 9 millimeters in length.

The following is a description of the mature larva of *Cephus pygmaeus* (*5*), illustrated in Figure 6.

The body is nearly cylindrical in outline. The head is of medium size, being much smaller than either of the thoracic segments. The thoracic segments are somewhat swollen; and the abdomen tapers gradually from the thorax to the caudal end. The antennae are four-jointed, and taper strongly. A short distance ventro-caudad of each antenna is a single black ocellus. The labrum is prominent and slightly emarginate. The mandibles are strongly toothed. The maxillary palpi are four-jointed. There are 10 pairs of spiracles, 2 thoracic and 8 abdominal. The prothoracic spiracles are much larger than the others and are greatly elongated. The second spiracles open in the fold between the mesothorax and metathorax. The remaining spiracles are borne by the abdominal segments one to eight. The thoracic legs are represented by very short tubercles. There is, at the caudal end of the body, on the middle line, dorsad of the vent, a prominent tubercle. This is terminated by a chitinous ferrule-like ring, and is doubtless an organ of locomotion. On each side of the ventral lobe at the caudal end of the body there is also a stout spine. These spines probably have the same function as the tubercle just described. The body is naked except the head and caudal extremity. There are a few slender scattered hairs upon the head, and a like quantity of stronger more spinelike hairs at the caudal end.

FIG. 6.—Drawing of larva of *Cephus pygmaeus*. Much enlarged.

The larvae of this species are likely to be confused with those of *Cephus cinctus* (Norton) and *Trachelus tabidus* (Fabricius). All three species infest small grain in practically the same manner. They may be distinguished one from the other by using the following key, which was worked out by A. B. Gahan (7), in conjunction with the illustration in Figure 7.

Key for separating grain-infesting sawfly larvae.

1. Dorsal anal lobe of the tenth tergite view from the side triangular, sloping gradually from base to apex, and the anterior end of lobe much thicker than the posterior end, which is more or less acute. Spines on the anal prong each arising from a small, more or less chitinized tubercle and closely grouped about the apex of the enlarged fleshy portion just basad of the short chitinized apical ring. Eighth and ninth tergites apparently glabrous 2

   Dorsal anal lobe viewed from side not triangular, not sloping gradually from base to apex but convexly rounded, the posterior end of the lobe as thick dorso-ventrally as the anterior end and nearly perpendicular. Anal prong completely encircled by two irregular series of widely separated, short stiff spines which do not arise from chitinized tubercles. Eighth and ninth tergites each with transverse row of distinct short hairs ..... *Trachelus tabidus* (Fabricius)

2. Anal prong terminating in a short chitinized ring which is not as long as broad. Spines basad of chitinized ring few in number, confined to a single transverse row on dorsal surface. Dorsal, lateral, and ventral lobes are sparsely hairy ..... *Cephus pygmaeus* (Linnaeus)

   Anal prong terminating in a chitnized tubelike process which is distinctly longer than broad. Spines basad of the apical tubelike process numerous, arranged in two irregular contiguous series completely encircling base of tube. Anal lobes distinctly hairy. *Cephus cinctus* (Norton)

PUPA

When the pupa (fig. 8) of *Cephus pygmaeus* first forms it is a milky white slender object that is between 10 and 12 millimeters long, and from 1 to 2 millimeters wide. It is quite motionless at first and does not move even if disturbed. About the second or third day it begins to slowly change its color, becoming darker. The body and legs gradually darken until it finally takes on the colors of the adult sawfly. The duration of this pupal period is not definitely known, but it seems probable that it lasts about a week.

ADULT

The adult (fig. 9) is a beautiful, shiny black insect, banded and spotted with yellow. The male and female are similar in color but vary somewhat in size. The male measures about 8 millimeters in length, while the female measures about 10 millimeters in length.

The body and appendages are covered with a large number of microscopic hairs, that are somewhat longer and denser, especially in the male, on the ventral and caudal parts of the abdomen. The head is large, with two prominent compound eyes. Three ocelli are present in the form of a triangle on the summit of the head. The antennae are on the front, nearly opposite the middle of the compound eyes, and are about 5 millimeters long, slightly clavate, and composed of 19 or 20 segments. The first segment is distinctly ovate, with a well marked bulb at the base that appears like a distinct globular segment. The second segment is short, being about as broad as long.

The next three segments are somewhat elongated; after this the segments become successively shorter until the middle of the antenna is reached, where they become wider than they are long. The last segment is somewhat longer and thus forms a supernumerary segment. The wings are four in number, and transparent and iridescent, but somewhat smoky. The costal margin of the wing is yellow toward the base. The subcostal vein, which is closely united to the costa, is, like the other veins, a dark brown color. There is a more or less well-marked smoky spot in the third discoidal cell extending from the origin of the posterior vein.

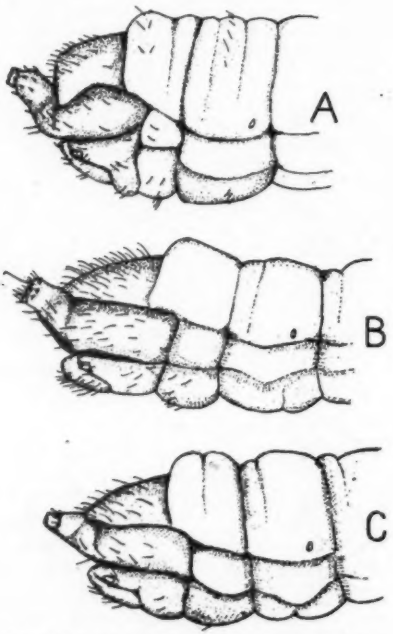

FIG. 7.—Lateral aspect of the apical segments of grain-infesting sawfly larvae. A, *Trachelus tabidus:* Lateral view of apical segments of larva; B, *Cephus cinctus:* Lateral view of apical segments of larva; C, *Cephus pygmaeus:* Lateral view of apical segments of larva. (After Gahan.) (Plate reproduced from U. S. Department of Agriculture Bulletin 834.)

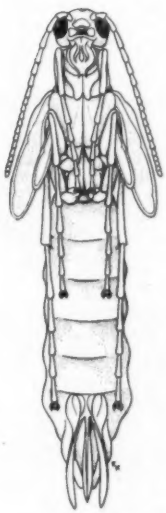

FIG. 8.—Drawing of pupa of *Cephus pygmaeus*. Much enlarged.

The yellow markings in the male are more prominent and more extended than in the female. The mouth parts, except the tip of the mandibles, which are dark brown; a spot on the clypeus; a narrow margin between the compound eyes and the mouth parts; the ventral side of the thorax; the legs, excepting a dark band on the caudal aspect of the coxae and femora (the tibia and tarsi are sometimes brown instead of yellow); the membrane at the base of the abdomen; on the ventral side of the abdomen the caudal margin of each segment; on the dorsal side of the abdomen a more or less well-

marked spot on each side of the first and second abdominal segments; a narrow band on the caudal margin of the sixth segment, which may be interrupted, and thus forming spots on the back and sides; and the latero-caudal angles of the seventh segment—are all yellow in the male insect.

In the female there is a yellow spot at the base of the mandibles; the maxillary palpi, except the terminal portions, are yellow; the tibia and tarsi may vary from a yellowish-brown to a dark-brown color; the markings of the abdomen are the same as in the male, with the exception that the yellow spots and bands are usually smaller, and may even be wanting in the ventral aspect.

FIG. 9.—Drawing of adult female of *Cephus pygmaeus*

Both the male and the female vary greatly in color and in the width of the bands on the abdomen. While collecting adults in the field in 1923, the writer found that the color of the markings varied from a bright, almost lemon-yellow through orange, until, in several instances, it closely approached a deep red. These color variations have also been noted in *Cephus cinctus*, a closely related species found in the western part of this country and Canada.

Since there is a great similarity between the adults of the different species of sawflies found in this country, P. R. Myers worked out the following key for the determination of the adults:

Key to adult grain-stem sawflies of the United States

1. Abdomen without dorsal, transverse, yellow bands; ovipositor sheaths when viewed dorsally swollen or laterally enlarged toward their apices; males with horseshoe-shaped depressions on the last two apical ventral segments ..... *Trachelus tabidus* (Fabricius)
   Abdomen with dorsal, transverse, yellow bands; ovipositor sheaths when viewed dorsally not swollen or laterally enlarged toward their apices; males without horseshoe-shaped depressions on the last two apical ventral segments 2
2. Stigma and costa dark brown of a uniform color; mesepisternum black; femora black; apical tergite and venter black; face and scutellum black (face of ♂ with yellow spots) ..... *Cephus pygmaeus* (Linnaeus)
   Stigma in greater part and costa yellow; mesepisternum with upper angle yellow; femora mostly yellow; apical tergite and usually venter in part yellow; face and scutellum of female usually black but occasionally with yellow spots ..... *Cephus cinctus* (Norton)

LIFE HISTORY AND HABITS

This insect has but one generation a year. The adult sawflies begin to appear, in the vicinity of Ithaca, about the first of June. In 1923 the earliest date of emergence was recorded by the writer as June 1. On May 26 no adults, so far as could be seen, had emerged in the fields on the Cornell University farm.

The adults remain at large in the fields until about the end of June, the 21st being the latest date that any were observed in the fields about Ithaca. In the fields near Batavia they were still quite abundant as late as June 26.

The meteorological conditions seem to have a great deal to do with the time of emergence. If warm, moderately dry weather follows the melting of the snow these insects will probably emerge sooner than if the weather during the spring is cold and damp. The adults are very active and able to take flight as soon as they have released themselves from the cocoon. In a number of instances the writer has broken open the hibernation chamber in a wheat stub and released the adult sawfly, which, when permitted, took to the air immediately.

Copulation takes place very soon after the adults have emerged, and usually lasts about ten minutes. It was interesting to note that copulation occurred, almost without exception, on yellow flowers that were growing either in the wheat field or along the edges of it. Most of these flowers belonged to the *Cruciferae* or mustard family. Only two instances were recorded where copulation took place on other flowers. One pair were found mating on the common "butter and eggs" (*Linaria vulgaris*), while another pair was observed copulating on the dewberry (*Rubus villosus*). The writer recorded only one instance where the copulation actually took place on a wheat plant. And in no case was it observed taking place while the insects were on the wing. The most common place to find these adults was on the common mustard (*Brassica nigra*).

It was very easy to obtain accurate notes on the habits of the adults because of their tameness and their partiality for yellow flowers. They were so easily approached that after the first day of collecting the writer did not use a net. It merely was necessary to find a patch of yellow mustard flowers, for there one was able to find both males and females in groups of 6 to 15. During the col-

lecting period between June 1 and 21, when the adults were flying, the writer collected nearly 1,000 specimens. Many times where there was a field of oats containing several stray mustard plants, the sawflies were found on these plants, although no wheat field was near by. The adults are most active on warm sunny days when there is little or no wind. If the day was windy or cool and cloudy, hardly an individual was observed in the field.

The oviposition habits of these insects are very interesting and much time was spent patiently waiting and watching for a female to settle down to oviposit. The reason for this delay was that the female of this insect seems to be very tidy and extremely particular about her personal appearance before she deposits an egg, as the following note, taken by the writer in the field June 16, 1923, will clearly show.

After hovering over the plant for some time, the female alighted on the curved-over blade of the topmost leaf of the plant. She stayed here for exactly 10 minutes by the watch. While resting on the leaf she held the body in a horizontal position and parallel with the edge of the leaf. Her head was pointed toward the end of the blade and the wings were folded along the back. Suddenly she became agitated and the abdomen was slightly curved upward, the wings were raised and held at right angles to the body and inclined at an angle of about 45°. This position was held for a few seconds and then she suddenly turned around as if to descend the stem. But before descending, she cleaned herself completely. The wings were preened and it seemed as if she even smoothed down all the hairs on her body. She brushed herself over and over with the most minute care. Indeed it became exasperating waiting for this female to finish her toilet, but finally after several more minutes delay she seemed ready to appear in public. She started slowly down the stem, taking a few steps at a time. Upon reaching a point about midway between the third and fourth nodes, she stopped, rested a few moments, and again seemed to smooth down all the hairs on her body. At this point her head was downward. The abdomen was curved so that the caudal end was nearly at right angles with the rest of the body. After thrusting her saw in and out of the stem several times, she withdrew it and inserted her ovipositor. The ovipositor was then withdrawn and the female flew away to another plant. Upon examination the stem showed only a slight puncture, but upon closer inspection this proved to be a crescent-shaped cut. The egg was found on the inside of the stem opposite the cut on the exterior.

Ainslie (*1*), in studying the western species, *Cephus cinctus*, has observed similar actions in the case of the female, thus indicating that the behavior of *Cephus pygmaeus*, as previously described, is common to these species.

The egg is laid within the stem of the wheat by the female sawfly in the manner already described. By watching this process carefully with a hand lens it was possible to see the female insert her saw, draw it out and insert the ovipositor. Curiously enough she did not object to this method of observation, so long as the observer made no sudden movement.

While one female lays but a single egg in a given wheat stem, other females may lay eggs in this same stem. The writer has collected stems immediately after a single female was observed ovipositing in them, and upon later examination as many as five eggs were found in a single straw. When the eggs are laid the head of the wheat has not yet appeared from the "boot" and usually the female oviposits just below the head, which at this time is between the third and fourth nodes. This, however, does not hold to be a hard and fast rule, as a number of eggs were found well down toward the root and

others still higher up in the stem. It is the opinion of the writer that the softness of the tissue of the stem partly determines the place of oviposition, as a female has been observed to try several places along the stem before finally ovipositing. Each female lays about 50 eggs.

The length of incubation is from 7 to 10 days. The method of determining this period was as follows: When a female was observed ovipositing in a stem, this stem was carefully marked at the place of oviposition and removed to the laboratory. The stem was then split and a small section about one inch long containing the egg was cut out. This section was split and the half containing the egg was placed in a small vial on a piece of moist blotting paper. The vial was then plugged with cotton and placed in a dark place where a fairly warm temperature of about 70° to 75° F. was maintained. It was examined each day, and the moisture in the vial was kept as near constant as possible. In this way a fairly accurate figure was obtained on the incubation period, which seemed to vary from 7 to 10 days, depending upon the meterological conditions.

When the larva first hatches, it has a large head, much out of proportion to the rest of its weak, slender body, the head being armed with a pair of powerful biting jaws. But all these imperfections, if they may be called such, are offset by its ravenous appetite, and, as has been pointed out before, it begins almost immediately to feed upon the delicate parenchymatous tissue lining the inside of the stem. As it reaches a node where more resistance is met to impede its progress, it excavates a tunnel through this and goes on to the next node. In examining a number of stems in which the larvae had been working it seemed that they must have traversed the tunneled stem several times during the season because they were found in nearly all parts of the stem with the frass of their work both above and below them. It was impossible, therefore, to determine accurately the number of instars, since only the chitinous head mask or a piece of the caudal horn remained, and these were very difficult to find when mixed in the frass within the stem. Upon careful examination the writer has been able to find these head masks and caudal horns in the débris, but in no case have more than four masks been found in a single stem, and very rarely was this number found. It is quite likely that there are either three or four instars of this insect.

From data collected on the approximate time of oviposition and the approximate time at which the larva spun its cocoon. it would seem that the period of growth covers about a month. Adults were introduced into a number of cages containing wheat plants during the first week of June. On June 18 the first larvae were found working in the stems. These larvae were about one week old when noted. On July 14 the first cocoons were found at the base of the wheat plants.

When the writer visited Batavia on June 26 he found larvae which seemed to be about a week old working in the stems. On July 23 in the same fields most of the larvae already had spun their cocoons near the roots of the grain plants. From these observations, it seems that about a month is required for the larva to complete its growth. Weather factors doubtless influence the rate of development. When the larva is mature and ready to build its

hibernation and pupation chamber it does its greatest damage to the grain plant.

When it reaches the base of the plant it cuts it off in a manner that has already been described. The cocoon spun by the larva is very flexible when first made, but becomes extremely brittle after being exposed to the cold weather during the winter months. It is closed at both ends, and is usually several times the length of the larva. During the winter the larva was found with its head pressed tightly against the top of the cocoon, and stayed in that position until disturbed, when it worked its way to the lowest part of the cocoon by the so-called "hitching" method that has been described. The gallery below the plug, although it appears to have been eaten out, is usually free from frass, such as is found in the rest of the stem where the larva has been working. The stems usually are cut off about ½ to 1 inch above the ground line. Figure 10 shows an infested stubble containing the overwintering larva. The side wall of the stem has been cut away and the cocoon torn apart in order to show the larva within. The black patch near the top of the stub is the lower plug. The upper edge of the stub is very ragged. This is characteristic of the manner in which the *Cephus pygmaeus* larva severs the stem.

FIG. 10.—Wheat stubble infested by *Cephus pygmaeus*

In the spring the larva changes to a pupa, but the length of this stage is not definitely known. It seems probable, from observations made by the writer, that this period covers about one week. In a field note under the date of June 5 it was noted that a number of cocoons that were opened still contained living larvae. At this date the adults had been flying about a week, and since the last adults to be observed or collected in the field were found on June 21, the pupal stage can not, therefore, be of very long duration.

It then changes to an adult, and works its way out through the plug above the cocoon. Thus we have the life cycle completed after the insect has been semidormant for nearly nine months.

PARASITES

The natural enemies of this insect both in this country and in Europe do not seem to be very common. Only two parasites are recorded as being found on it in Europe, while in this country there have been seven recorded by the writer. Comstock recorded a "single crippled female ichneumon fly," and W. R. McConnell reared a single specimen of *Eupelmus allynii* (French) from a Cephus infested stub of wheat collected near Victor, N. Y., in 1919.

The following parasites are recorded in European literature as being natural enemies: *Collyria calcitrator* (Gravenhorst); *Arthrolysis scabricula* (Nees).

The following is a list of the parasites reared in this country from *Cephus pygmaeus; Eupelmus allynii* (French); *Eupelminus saltator* (Lindemann); *Pleurotropis benefica* (Gahan); *Eurytoma* species; *Heter-*

ospilus cephi (Rohwer); *Hoplocryptus* new species; *Epiurus* new species(?).

All the parasites in the above list have been reared from *Cephus pygmaeus* material by the author from material collected by C. R. Crosby and himself in New York State.

SUMMARY

The wheat-stem sawfly *Cephus pygmaeus* (Linn.) was first recorded in 1762 by Geoffroy and named *Tenthredo* species. In 1767 it was described by Linnaeus as *Sirex pygmaeus*, but in 1802 it was given its present name of *Cephus pygmaeus* by Latreille.

It was first recorded in this country from the vicinity of Ithaca, N. Y., by J. H. Comstock in 1887. It seems to have escaped attention for some time after that, but within the last few years has again been brought to the attention of entomologists.

Cephus pygmaeus has, so far as known, a limited distribution. It is recorded from 13 countries of Europe and Asia. In the United States it has been collected from 20 counties of New York and 14 counties of Pennsylvania.

Its food plants are few in number, those recorded up to the present being only wheat, barley, rye, and chess. Although numerous other grains and grasses have been examined, none have been found to be infested with the sawfly larvae.

The injury produced is rather characteristic. The female deposits the egg within the stem early in June just before the head leaves the "boot." The larva after hatching works its way down the stem, eating the tissue that lines the interior walls, until a point about ½ or 1 inch above the ground is reached. It then forms a plug of excrement and frass in the cavity. Immediately below this plug it cuts a V-shaped groove around the interior of the culm, leaving only the epidermis uncut. Below this plug it places another plug of the same material, to the underside of which it attaches its hibernation cocoon.

There is but one generation a year, the adults emerging the latter part of May or early in June, after which the eggs are deposited. These hatch in 7 to 10 days, and the larvae feed for about a month before they cut the stem off and go into hibernation for the winter, spending about 9 months in a semidormant stage. Pupation takes place in the spring about a week before the adults emerge.

Cephus pygmaeus has but few natural enemies, there being only 7 recorded in this country and two in Europe, all of which have been listed in this paper.

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